THE GREATER ANTILLEAN INSECTIVORES

SAMUEL BOOKER MCDOWELL, JR.

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PREFACE

THE PRESENT PAPER, dealing with the affinities of *Solenodon* and *Nesophontes*, is the by-product of a more extensive series of researches in the anatomy and relationships of the fossil Leptictidae. In the course of comparing the leptictids with modern insectivores I was surprised to discover that the same specialized features that set the Erinaceidae apart from the leptictids were also present in the Talpidae, Soricidae, Nesophontidae, Solenodontidae, Tenrecidae (including *Potamogale*), and Chrysochloridae. Further, I found that this same suite of characters distinguished these modern insectivore families (so far as comparisons are possible) from the Zalambdalestidae, Pantolestidae, Apheliscidae, Mixodectidae, Apatemyidae, Deltatheridiidae, Palaeoryctidae, and Apternodontidae. From this, I was forced to conclude that the modern insectivores formed a truly natural group, a conclusion in which I was anticipated by many previous workers, notably W. K. Gregory, who recognized the Lipotyphla as a natural order of mammals.

Unknown to me at the time, Dr. P. M. Butler in England was simultaneously making anatomical comparisons between the Leptictidae and other insectivores. His results have now been published (1956) and on this point are essentially the same as my own, that the Lipotyphla are a natural and relatively homogeneous group of mammals.

Because of a suggestion by W. K. Gregory in 1910 that *Solenodon* shows special resemblance to the Leptictidae, I paid special attention to this peculiar West Indian insectivore. The result of this special attention is the present paper.

The parallel investigations of Dr. Butler led him to the same conclusion as mine, that the two West Indian insectivores, *Solenodon* and *Nesophontes*, are closely related, albeit they show dental differences that have been regarded as of superfamily (or even higher) value in the taxonomy of the group. Because of the chronological accident that I reached this conclusion about a year before Dr. Butler did, he most generously relinquished publication to me. It should be understood, however, that these researches were carried on quite independently and that Dr. Butler is in no way responsible for any errors in the following pages.

My thanks go to Dr. George Gaylord Simpson, of Columbia University and the American Museum of Natural History, for sponsoring the research and suffering most graciously the numerous annoyances such sponsorship involved. Dr. Bobb Schaeffer of the American Museum of Natural History has given me the benefit of his advice and time in the reading of the manuscript. Mrs. Rachel Nichols, Department of Geology and Paleontology, the American Museum of Natural History, has been of invaluable assistance in obtaining both biological and literary material for me.

In the Department of Mammals of the American Museum of Natural History, the courtesy of Dr. Harold Anthony, of Mr. T. Donald Carter, and of Mr. George Goodwin has made possible the present work. Dr. Joseph Curtis Moore, in addition to other courtesies, has given me the benefit of his knowledge of living shrews in captivity. Miss Gabriele Neuhauser and Mr. Hobart Van Deusen have generously put the fine series of Malagasy insectivores in the Archbold collection at my disposal.

Whatever merit the drawings in this paper possess is the result of the advice of Mr. Chester Tarka of the Illustrator Corps of the American Museum of Natural History.

Dr. Lewis Gazin of the United States National Museum has been most kind in furnishing material of fossil insectivores, while Dr. Glenn L. Jepsen has shown me the remarkable fossil material in the collections of Princeton University. Conversations at Princeton with Dr. John Clark have aided me immeasurably in my researches. Dr. Joseph Gregory of the Yale Peabody Museum has read the manuscript and given invaluable advice.

Mr. Malcolm McKenna, University of California (Berkeley), has given me the benefit of his extensive knowledge of early Tertiary insectivores, and demonstrated important undescribed cranial material.

Dr. Karl F. Koopman of Queens College,

New York, has most graciously criticized the manuscript and given me much information on West Indian zoogeography and on dental variation in Chiroptera.

Dr. James Bump of the South Dakota School of Mines has lent me excellent leptictid material that has formed the basis of my initial researches.

Dr. Ernest E. Williams of the Museum of Comparative Zoölogy of Harvard College has been most informative on West Indian zoogeography and, besides extending numerous other courtesies, has criticized the manuscript. My thanks are also due to Prof. Bryan Patterson, Harvard University, for reading a first draft of the manuscript and for his most interesting and revealing comments. The staff of the department of mammals at the Museum of Comparative Zoölogy has most courteously allowed me examination of what is perhaps the most complete sampling of living insectivore genera in the United States. In addition they have provided the author with three preserved *Solenodon paradoxus*. While a strike of express workers caused these specimens to arrive in something less than perfect condition, they nevertheless have allowed a study of the basicranium that would otherwise have been impossible.

The advice, aid, and encouragement of various members of the Department of Zoology, Columbia University, have come from so many sources over so long a time that many people must be omitted from acknowledgment quite unjustly. All that can be said is that Dr. Francis Ryan and Dr. Franz Schrader have been of most recent assistance. I also thank Dr. Edwin Matzke of the Department of Botany of Columbia University.

I am particularly grateful to Dr. M. LaMotte for a mold of the skull and jaw of *Micropotamogale lamottei*.

The assistance of my wife, Rosa McDowell, in the preparation of the manuscript has made the present paper possible.

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INTRODUCTION

THE LIMITED NATIVE MAMMALIAN fauna of the Greater Antilles includes the Orders Insectivora, Primates, Chiroptera, Edentata, and Rodentia. Of these, the insectivores are perhaps of the greatest interest, for they are the only Antillean group of indisputably North American origin and are also the most sharply distinguished endemic mammals of the West Indies. Current classification (as Simpson, 1945) places each of the two genera of Antillean insectivores, *Solenodon* and *Nesophontes*, in a separate family without continental representatives among modern faunas. The Nesophontidae are, in fact, a strictly monogeneric family, known only from the sub-Recent of Cuba, the Isle of Pines, Ile de la Gonave, Hispaniola, and Puerto Rico. The Solenodontidae are now represented by but two species, one from Cuba (sometimes referred to a separate genus, *Atopogale* Cabrera), and one from Hispaniola; however, certain North American Oligocene genera (*Apternodus*, *Clinopternodus*, and *Micropternodus*) have been referred to the Solenodontidae.

As to the broader affinities of the Nesophontidae and Solenodontidae, the former family is generally regarded as closest to the Soricidae, while the Solenodontidae are generally grouped with the Afro-Malagasy Tenrecidae, Potamogalidae, and Chrysochloridae (when this last family is not segregated into a superfamily or suborder of its own). This classification, based mainly on dentition, suggests only a remote affinity of the two West Indian genera with each other, and has the zoogeographical implication that there have been two quite separate invasions of the West Indies by insectivores.

One author, G. M. Allen (1918), has questioned this prevailing view and pointed out that in most features of osteology *Solenodon* and *Nesophontes* are very similar, and that the dental differences are not irreconcilable.

In the following pages, the present author presents his arguments for believing that (1) *Solenodon* is, indeed, very closely related to *Nesophontes*; (2) both genera are closely related to the Soricidae and form with that family a sharply defined natural division of the lipotyphlous Insectivora; (3) the resemblance in dentition between the Afro-Malagasy tenrecs and *Solenodon* is the result of convergence and of no more phylogenetic weight than the resemblance of both groups to the equally zalambdodont Australian marsupial *Notoryctes*; and (4) the Oligocene North American forms referred to the Solenodontidae are not related to *Solenodon* and, indeed, are not even lipotyphlous insectivores.

SOME DEFINITIONS

The following list of definitions is not an attempt at a complete glossary of the skull of mammals. Rather, it is a set of definitions used in the present paper for one group of mammals, the Lipotyphla. The only terms included are those that are (1) rarely used in mammalogy; or (2) expanded or restricted in definition to fit the special problems of describing the dried skull of the adult lipotyphlan; or (3) used in so many different senses by different authors as to create confusion; or (4) coined here by myself.

The authors quoted here for many of the terms are not the first users of the terms (indeed, some terms go back to Galen), or even the first to give definitions. Rather, the citations and quotations refer to well-known references in English with illustrations (Van der Klaauw's illustrations are in the last section of his paper that describes his original observations).

There are two ways to define an anatomical structure. The first, or geometrical, method consists of one's listing its characteristic connections on the assumption that any structure with these connections is to be called by the particular name that is being defined.

The second, or phylogenetic, method essentially chooses a type animal to exhibit the named structure, then attempts to find the

corresponding structure, by any and all available clues, in the forms phylogenetically related to the type.

Both methods of definition are useful, depending on the problem at hand. When the problem is to determine a phylogeny, then the geometrical (or "*Gegenbaurian*") method must be used to avoid circularity. But because connections may change with evolution, when the phylogeny is reasonably certain the second method is preferable, particularly in purely anatomical problems for which it is desired to keep nomenclature as simple as possible.

The maker of a glossary is always drawn towards the geometrical definition, for such a definition lends itself most easily to the written paragraph. For this reason, I have been forced in some cases to invent geometrical definitions for some structures that are perhaps better defined in phylogenetic terms. My only apology is to point out that such a definition of entoglenoid process as "the process corresponding to the entoglenoid process of *Lemur*" leaves the user of a glossary no better informed than he was before thumbing the pages.

Alisphenoid Canal

"For the external carotid. Posterior opening in front of foramen ovale; tunnels or grooves alisphenoid and, running forwards, sometimes becomes confluent with the foramen rotundum (e.g., *Canis*) but sometimes opens separately (Rodents)" (Gregory, 1910, p. 430).

Aqueductus Cochleae (Canaliculus Cochleae)

A canal in the petrous bone for the perilymphatic duct and cochlear vein. (Schaeffer, 1942, p. 148.)

Aqueductus Vestibuli

A canal in the petrous bone for the endolymphatic duct of the membranous labyrinth of the ear. (Schaeffer, 1942, p. 119.)

Arteria Promontorii

The mesial branch of the internal carotid artery given off at the first branching of the carotid within the "bulla" or middle ear. It runs diagonally across the bulge of the promontorium. (Gregory, 1920a, pp. 171–174, figs. 64–65.)

Arteria Stapedia (Stapedial Artery)

The lateral branch of the internal carotid given off at the first branching of the carotid within the middle ear. It passes between the crura of the stapes, thus perforating that bone and then, typically, divides into two branches, a ramus superior and a ramus inferior. (Gregory, 1920a, pp. 171–174, figs. 64–65.)

Attic (Atticus Tympanicus)

Equivalent to epitympanic recess. (Van der Klaauw, p. 73.)

Auricular Nerve (Nerve of Arnold)

A nerve from the jugular ganglion of the vagus joining the facial nerve, or lying in contact with it. A sensory nerve, it supplies posterior and inferior parts of the external auditory meatus and the pinna and the lower part of the outer surface of the eardrum (*Homo*). (Schaeffer, 1942, pp. 1078–1079.)

Bullar Wing

A general term here used for a bony shelf forming a floor to the middle ear in the dried skull. Thus, the bullar wing of the basisphenoid is a plate of bone developed from the basisphenoid and closing the middle ear ventrally.

Capitular Surface

The surface of the "condyloid process" or condyle of the dentary for the fibrocartilage of the articulation (Schaeffer, 1942, p. 167, "capitulum"). Here used to include the opposing surface or surfaces on the squamosal. The term is *not* equivalent to condyle, but refers only to that portion of the condyle immediately abutting against a joint apparatus of fibrocartilage.

Cavum Epiptericum

" . . . An extracranial (i.e., outside the dura mater) space situated laterally to the side wall of the orbitotemporal region of the skull, dorsally to the basitrabecular process, and medially to the processus ascendens of the pterygoquadrate cartilage. The cavum epiptericum thus lodges the ganglia of the trigeminal and facial nerves, and is traversed by their branches and by the abducens nerve, the head vein, and the orbital (or stapedial) artery. It includes the sinus cavernosus in mammals." (De Beer, 1937, p. 430.)

Chorda Tympani

A mixed nerve, although mainly sensory, running from the facial nerve through the middle ear medial to the malleus, thence through the fissure

between the tympanic and petrous bones ultimately to join the lingual nerve (a branch of the mandibular ramus of the trigeminal) and to supply the anterior taste buds of the tongue (*Homo*). (Schaeffer, 1942, pp. 1068–1069.) It may be added that in most Lipotyphla this nerve passes through the Folian process of the malleus.

Chordafortsatz

"This element conducts the chorda tympani nerve from its entrance in the tympanic chamber toward the malleus. It is often bony, sometimes partly or totally cartilaginous and can be free or attached to the different elements in the hinder part of the tympanic chamber." (Van der Klaauw, 1931, pp. 207–208.)

Condyloid Canal

A canal for a vein on the medial side of the occipital bone, in the wall of the foramen magnum. (Sense of Sisson, 1938, p. 131, fig. 135.) Not to be confused with condylar foramen, a name sometimes given to the foramen for the hypoglossal nerve.

Cribriform Plate

The transverse plate of the ethmoid bone pierced by filaments of the olfactory nerve. (Schaeffer, 1942, pp. 152–153.)

Dorsum Sellae

"The posterior boundary of the sella turcica (fossa for the pituitary gland) is formed by a quadrilateral plate of bone, the dorsum sellae." (Schaeffer, 1942, p. 136.)

Ectopterygoid Lamina

The name given here to the lamina of the alisphenoid extending outward between the external and internal pterygoid muscles; the lateral pterygoid plate of Schaeffer (1942, p. 139).

Entocarotid (Artery)

A brief form of "internal carotid artery," used, for example, in Gregory (1910).

Entoglenoid Process

The name used by Gregory (as in 1910, p. 244) for a process of the squamosal situated behind the glenoid fossa and continuous with the preotic crest of the alisphenoid (tympanic crest of the alisphenoid of Gregory). It can scarcely be homologous with the processus postglenoideus, as many mammals possess *both* the entoglenoid process and the processus postglenoideus; this is described and figured, for example, in *Notharctus* by Gregory (1920a, p. 158, pl. 44). The entoglenoid process lies on that portion of the squamosal unrepresented even in therapsid reptiles: the wing extending mesiad, anteroventral to the otic capsule, to meet the epiterygoid (alisphenoid). It thus lies mesial to Meckel's cartilage and the companion of that structure, the chorda tympani. It attacks the condyle of the dentary from a posteromesial, rather than directly posterior, position. It lies directly beneath the posterior part of the cavum epiptericum and does not extend outward from the braincase onto the zygomatic arch. Hence, it lies on a more median parasagittal plane than does the postglenoid foramen (for the juncture of the external jugular vein and superior petrosal sinus). Except for those mammals in which it is modified to clasp the dentary, or else absent altogether, it is merely the continuation onto the squamosal of the preotic crest of the alisphenoid.

Entotympanic

"Under this name we take together all the skeletal elements, bony or cartilaginous, that lie in the ventral wall of the tympanic cavity and are ontogenetically primarily independent of the other elements in the auditory bulla, except perhaps the tympanohyal and the cartilage of the Eustachian tube." (Van der Klaauw, 1931, p. 266.) As used in the present paper, the name is restricted to an endochondral bone homologous with the "entotympanic" of *Tupaia*.

Epitympanic Recess

" . . . That part of the primary tympanic cavity which in the mammals was added to this cavity when the elements of the joint of the jaw in the lower vertebrates were received into this cavity with the function of auditory ossicles. . . . The recessus epitympanicus is covered on the medial side by the tegmen tympani of the periotic, which is also a neomorph in the mammals, also by the squamosal, while the lateral wall is very differently developed." (Van der Klaauw, 1931, p. 73.)

Epitympanic Wing

A name here given to the process of the alisphenoid contributing to the roof of the middle ear cavity, to avoid confusion with the "tympanic wing of the alisphenoid" of marsupials, a process contributing to the *floor* of the middle ear.

Ethmoidal Foramen (Foramina)

"For the *entry* of the nasal nerve (a branch of V_1) and ethmoid artery" into the ethmoid region from the orbit. (Gregory, 1910, p. 430.)

External Capitular Facet

A name given here to the more lateral of the two capitular facets of the jaw articulation seen in the Soricidae and Solenodontidae.

Fallopian Aqueduct (or Canal)

The canal through the petrosal bone for the facial nerve. (Schaeffer, 1942, pp. 149, 1063.)

Fenestra Ovalis (Fenestra Vestibuli)

The perforation in the wall of the ear capsule (petrosal bone) for the foot-plate of the stapes. (De Beer, 1937, p. 400.)

Fenestra Rotunda (Fenestra Cochleae)

A foramen in the petrosal bone of mammals leading into the cochlea. According to De Beer (1937, p. 402), it is formed by the backgrowth of the cartilaginous floor of the cochlear capsule from the anterior border of the foramen perilymphaticum. The aqueductus cochleae and fenestra rotunda are thus formed, so that in mammals, except monotremes, there are two entrances to the foramen perilymphaticum.

Folian Process

"The *processus anterior* (Folii, gracilis) of the malleus may with reasonable certainly be regarded as in part formed of the homologue of the prearticular . . . of reptiles, and birds. . . . It is a *membrane bone* situated on the medial side of Meckel's cartilage, and the chorda tympani nerve runs forwards between the two, which is a characteristic relation." (De Beer, 1937, p. 441.)

Foramen Lacerum Anterius (Anterior Lacerate Foramen)

Equals sphenorbital fissure or sphenorbital foramen. "Nerves III, IV, V_1, VI, and sometimes II." (Gregory, 1910, p. 429.) In Lipotyphla, as in many other mammals, the foramen lacerum anterius is confluent with the foramen rotundum of primates, carnivores, and marsupials; thus it also contains nerve V_2.

Foramen Lacerum Medium (Middle Lacerate Foramen)

This is the foramen lacerum anterius of those who call the foramen for nerves III, IV, V_1, and VI the "sphenorbital fissure." "In the Dog the internal carotid runs forward through an entocarotid canal lying between the tympanic bulla, the petrosal and the basisphenoid, and enters the cranium through the foramen lacerum medium." (Gregory, 1910, p. 430.) This use of the term, for the entrance of the carotid artery into the skull, is the usual one. However, Story (1951) redefines the names of the foramina for carnivores and restricts "foramen lacerum medium" to a *venous* foramen for the "large vein from inferior petrosal sinus, draining to pharyngeal and pterygoid plexuses," and calls the intracranial entranceway of the carotid the "anterior carotid" foramen. This use may not be puristically sound, but it is a very convenient one. As the carotid of carnivores is probably not homologous with that of man (an arteria promontorii), it is questionable whether Gregory's use of a term from human anatomy is "puristically sound," although it is customary.

Foramen Lacerum Posterius (Posterior Lacerate Foramen)

"Nerves IX, X, XI." (Gregory, 1910, p. 430.) In the animals discussed in the present paper, the jugular vein passes through this same opening of the dried skull, so jugular foramen and foramen lacerum posterius are used interchangeably. This is not the case in all mammals, at least for the entire course, and Story (1951) makes a distinction between the nervous foramen lacerum posterius and a venous jugular foramen, the latter leading to the inferior petrosal sinus.

Foramen Ovale

"Nerve V_3. . . . The foramen ovale always looks toward the inner face of the mandible, since it gives exit to the mandibular branch of the trigeminus nerve." (Gregory, 1910, p. 429).

Foramen Stylomastoideum Definitivum

An outermost exit from the skull for the facial (VII) nerve that is bounded by the bulla. Where there is no expansion of the tympanic (or entotympanic) to form a bulla this foramen is not formed and the stylomastoid foramen is the foramen stylomastoideum primitivum. (Usage of Van der Klaauw, 1931, pp. 171–179.)

Foramen Stylomastoideum Primitivum

The passageway for the facial (VII) nerve between the tympanohyal, mastoid, and (often) the tympanic or the hyoid. In fetal mammals, and the adults of many mammals as well, this is the most external orifice for the facial nerve. However, in most mammals with an inflated bulla, the facial nerve, after passing through the foramen stylomastoideum primitivum, must then pass through a bony canal between the mastoid and the bulla to emerge finally from the foramen stylomastoideum definitivum (*q. v.*). (Usages of Van der Klaauw, 1931, pp. 171–179.)

Foramen Vesalii

A foramen of variable occurrence in man, located just anterior to the foramen ovale, and transmitting an emissary vein from the cavernous

sinus to the pterygoid plexus. (Schaeffer, 1942, pp. 138, 707.) The name is here given to the opening of the transverse canal in the belief that the foramen Vesalii of man is a vestige of a transverse canal, as indicated by its position and its transmission of a vein to the pterygoid (venous) plexus.

Gasserian Fossa

A term coined here for the bony portion of the cranial cavity containing the Gasserian ganglion of the trigeminal (V) nerve. It is used in preference to cavum epiptericum because the limits of the latter cavity can be determined precisely only by examination of the attachments of the dura mater, not available in the dried skull. As here proposed, Gasserian fossa would refer to a depression in the alisphenoid (as seen from within the cranial cavity), this depression containing the openings of the foramen ovale, foramen rotundum, and foramen lacerum anterius.

Gasserian Ganglion

The ganglion of the fifth nerve, also called the semilunar ganglion. (Schaeffer, 1942, p. 944.)

Glenoid Fossa

The fossa of the squamosal for the reception of the condyle of the dentary.

Great Superficial Petrosal Nerve

A nerve made up of visceral afferent and visceral efferent fibers, arising from the facial (more precisely, the intermediate nerve of the facial) and escaping from the Fallopian aqueduct through a foramen in the petrosal (the "hiatus Fallopii") to enter the middle-ear chamber to form the major portion of the Vidian nerve. (Schaeffer, 1942, p. 1068.)

Hamular Process

This term is restricted here to a conspicuously hook-like projection of the internal pyterygoid lamina.

Hypoglossal Foramen

The foramen in the occipital for the emergence of the hypoglossal (XII) nerve from the cranial cavity. The names "condylar foramen" and "condyloid foramen" are not used here, because of the possible confusion with the condyloid canal for a vein.

Hypophyseal Fossa

The fossa on the dorsal (intracranial) surface of the basisphenoid for the pituitary gland. (Schaeffer, 1942, p. 118.)

Incisive Foramen

A (paired) foramen in the bony palate behind the upper anterior incisors (thus bordered mainly by the premaxilla) for Stenson's duct (the duct of the organ of Jacobson). (Schaeffer, 1942, p. 1371.)

Inferior Petrosal Sinus

A venous dural sinus running from the cavernous venous sinus back to join with the internal jugular, lying essentially between the petrosal and basioccipital bones. Posteriorly it passes between the glossopharyngeal (IX) and vagus (X) nerves. (Schaeffer, 1942, p. 714.)

Infraorbital Canal

A canal in the maxilla, running from the orbit to the lateral surface of the muzzle, for the infraorbital nerve [a branch of the maxillary ramus of the trigeminal (V) nerve]. (Schaeffer, 1942, p. 159.)

Infraorbital Foramen

The anterior orifice of the infraorbital canal. (Schaeffer, 1942, p. 159.)

Inion

As here used, the occiput as defined by muscular scars and ridges for neck muscles.

Internal Auditory Meatus

For nerves VII and VIII, on the intracranial surface of the petrosal. (Gregory, 1910, p. 430.)

Interpterygoid Fossa

The continuation of the choanal passage between the pterygoid laminae posterior to the false palate.

Jugular Foramen

See foramen lacerum posterius.

Jugular Process

The "paroccipital" process of mammals.

Lacrimal Foramen

The perforation (or perforations) for the nasolacrimal (tear) duct. (Gregory, 1920b, p. 214.)

Lacrimal Tubercle

A projection on the lacrimal, usually just external to the foramen, for the tarsal ligament of the eyelids (Gregory, 1920b, p. 214.)

Lateral Facet of Occipital Condyle

A name given here for the articular facet of the occipital condyle placed lateral to the foramen magnum and facing caudad.

Mastoid

As here used, the posterior portion of the petrosal bone, essentially that portion of the bone posterior to a line joining the foramen stylomastoideum primitivum and foramen lacerum posterius.

Meatal Surface

As used here, a surface of bone (the squamosal bone unless otherwise stated) abutting against the tissue of the external auditory meatus.

Meatus

Unless otherwise modified, the word meatus is used here to mean the external auditory meatus.

Middle Meningeal Artery

A branch of the ramus superior of the stapedial artery (Gregory, 1920a, p. 172.) As used here, "middle meningeal artery" refers to all branches of the ramus superior of the stapedial artery that lie in the dura mater, within the cranial cavity.

Nasopalatine Foramen

The sphenopalatine foramen.

Nuchal Crest

In the animals here discussed, what is termed the "nuchal crest" appears to correspond with the structure seen in *Equus*, and the following remarks (Sisson, 1938, p. 51) apply: "The nuchal crest of this description is equivalent to the external occipital protuberance and superior nuchal line of man; it has been commonly termed the occipital crest, but is not the equivalent of that feature of the human skull."

Optic Foramen

"Nerve II." (Gregory, 1910, p. 429.) This foramen is in the orbitosphenoid bone and is set off from the foramen lacerum anterius by a usually slender bar of the orbitosphenoid (pila metoptica). Sometimes the foramen is present and defined by the pila metoptica, but lies deep within the foramen lacerum anterius (e.g., most Soricidae), and is then said to be absent by some authors. Or the pila metoptica may be absent, so that these foramina are confluent; this condition is also described as "optic foramen absent" by many authors. Finally, in some Chrysochloridae it appears that the optic nerve is absent, and the optic foramen is correspondingly lacking in the strictest sense.

Orbital Wing

As here used, the orbital wing of the palatine or maxilla is a lamina of the bone clasping the ethmoid and forming part of the wall of the orbit. In some animals (e.g., *Potamogale*) with a very small orbital wing of the palatine (as here defined) the palatine may still make a considerable contribution to the wall of the orbit, as the choanal passage has an abnormally dorsal position and the vertical lamina of the palatine (bounding the choanal passage laterally) contributes to the eye socket.

Orbitosphenoid

See presphenoid. This is an ossification of the chondrocranium proper (in contrast to the alisphenoid, an ossification of the palatopterygoid cartilage) formed in the vicinity of the optic nerve. There does not appear to be any genuinely objective line of external demarcation between the rear of the ethmoid and the front of the orbitosphenoid in the adult skull, and future workers may find it convenient to limit "orbitosphenoid" to the derivatives of pila metoptica (a bar of bone or cartilage just behind the optic nerve; De Beer, 1937, p. 388) and that portion of the endochondral bony orbital wall posterior to the attachment of the cribriform plate.

Paroccipital Process

A process of the exoccipital extending outward and downward behind the petrosal (general usage, as in Gregory, 1910; Matthew, 1909). Because the name "paroccipital" is frequently given to a nonhomologous element of the reptile skull (the opisthotic), many authors prefer, with reason, the name "jugular process" for the mammalian structure.

Periotic

Same as petrosal.

Petromastoid

Same as petrosal.

Petrosal

The entire bone formed by ossification of the otic capsule and its various processes. Because in man the petrosal, squamosal, and tympanic bones are fused into one, it is usual in human anatomy to refer to this bone as the "petrous portion of the temporal bone."

Petrous Bone

Same as petrosal.

Posterior Clinoid Process

A knob-like prominence on the superior angle of the dorsum sellae, giving attachment to the tentorial membrane. (Schaeffer, 1942, p. 136.)

Posterior Lacerate Foramen

See foramen lacerum posterius.

Posterior Palatine Canal

As here used, a canal (sometimes so short that it might better be called a foramen or even a mere emargination) in the palatine bone near the suture of the latter with the maxilla, just behind the last upper molar. Because of the variability of this region in the Class Mammalia it is not certain, perhaps is even unlikely, that the "posterior palatine canal" of various mammalian orders is homologous, but the name is used here as a convenience to indicate a relatively constant structure of the lipotyphlans.

Posterior Superior Recess

"Between the nasoturbinal and the second endoturbinal there develops a blind sac (recessus posterior superior) in which ectoturbinals form. On this view, what appears to be the line of attachment of the second endoturbinal to the cribriform plate should rather be regarded as the wall dividing the recessus posterior superior from the main part of the nasal cavity." (Butler, 1948, p. 496.)

Postglenoid Capitular Facet

A name given here to the more mesial of the two capitular facets of the squamosal-dentary articulation in the Soricidae and Solenodontidae.

Postglenoid Foramen

A foramen in the squamosal behind the glenoid fossa, transmitting the internal facial vein (of the external jugular system) from the superior petrosal sinus. (Story, 1951, p. 513.)

Postglenoid Process

As used in this paper, any kind of projection of the squamosal forming a posterior brace for the squamosal-dentary articulation. A "true postglenoid process," however, means a processus postglenoideus, which see.

Postmastoid Foramen (Mastoid Foramen)

A venous foramen in the petrosal bone, on its occipital (mastoid) surface. (Usage of Denison, 1938, fig. 19 on p. 211, "postmastoid foramen"; text on p. 215, "mastoid foramen.")

Postpalatine Torus

A term coined here (to my knowledge), for the transverse bony thickening at the rear of the bony palate.

Posttympanic Process

A process of the squamosal forming the posterior boundary of a notch in that bone for the external auditory meatus. (Usage of Gregory, 1910.)

Preotic Crest

A term used here for the raised crest of the alisphenoid forming a rim for the middle ear and connected laterally with the entoglenoid process of the squamosal. Equivalent to the "tympanic crest" of Gregory, 1910, but that term is not used here, because the crest does not meet the tympanic bone in insectivores (but does in marsupials).

Presphenoid

As here used, a median structure of the endochondral cranium anterior to the basisphenoid and formed by the fusion of mediad extensions of the two orbito-sphenoids. I here accept the statements of Roux (1947) as to the developmental facts of the case, but regard Roux's attempt to retain Broom's nomenclature as unnecessarily complex. Therefore, I use "mesethmoid" to mean an ossification of the nasal septum, universally present among mammals, and "presphenoid" for a median juncture of the orbitosphenoids that may be present (e.g., most Lipotyphla, Primates) or absent (e.g., Chrysochloridae, Marsupialia).

Processus Postglenoideus

Here used to mean a "true postglenoid process" homologous with that of man. That is, a process of the squamosal on the zygomatic arch, near the juncture of the latter with the braincase, abutting against the posterior surface of the dentary condyle and attacking the latter from directly posterior. The process lies mainly or entirely dorsolateral to the Meckelian cartilage and chorda tympani and is anterior or anterolateral to the postglenoid foramen (when the latter is present). See entoglenoid process.

Promontorium

A bulge on the ventral surface of the petrosal produced by bulging cochlea contained within. (Schaeffer, 1942, p. 1230.)

Pterygoid

As here used, the term applies only to the internal pterygoid lamina, a structure certainly formed from the pterygoid bone in most, if not all, mammals. The early obliteration of pterygoid-alisphenoid sutures in the insectivores renders it impossible to say what other structures are also parts of the pterygoid bone; for convenience, these are arbitrarily assumed to be part of the alisphenoid and basisphenoid.

Pterygoid Canal (Vidian Canal)

A canal in the sphenoid for the transmission of the Vidian nerve and accompanying artery. (Schaeffer, 1942, p. 139.)

Pterygoid Fossa

A fossa formed for the origin of the pterygoid muscles. (Gregory, 1910 p. 424.)

Pterygoid Lamina

A downwardly projecting plate of bone from the sphenoid continuous anteriorly with the vertical lamina of the palatine (equivalent to the lamina medialis processus pterygoidei of Schaeffer, 1942, p. 139.)

Pyriform Fenestra

A name given here to the large vacuity in the roof of the middle ear (corresponding to the area of origin of the tensor tympani) of the Soricidae and Solenodontidae.

Ramus Inferior (of Stapedial Artery)

A branch of the stapedial artery running forward in a groove on the roof of the tympanic cavity to enter the temporal fossa (there joining with the internal maxillary branch of the external carotid and entering the alisphenoid canal). (Gregory, 1920a, p. 172.)

Ramus Superior (of Stapedial Artery)

A branch of the stapedial artery, given off lateral to the passage of the latter between the crura of the stapes, that enters the cranial cavity. (Gregory, 1920a, p. 172.)

Recessus Meatus

The most proximal part of the bony external auditory meatus, set off from the meatus proper by its broader diameter. (Van der Klaauw, 1931, p. 137.)

Sinus Canal

A term, apparently first used by Parker (1886), for a canal or groove on the inner surface of the parietal for a vein running from the superior petrosal sinus to join with the ophthalmic veins in the orbit, and also for the middle meningeal artery as it passes forward to join with the ophthalmic arteries. The foramen by which the sinus canal opens into the orbit has no better name than "sinus canal foramen" (or, where context prevents confusion, simply "sinus canal"). Gregory (1910, p. 274) uses the name "supraorbital foramen," apparently in reference to its position above the orbital fissure (foramen lacerum anterius), but this leads to confusion with a very different foramen in the frontal above the orbit. The human foramen spinosum has the same approximate position and also gives passage to the anastamosis between ophthalmic and middle meningeal arteries.

Sphenoid Sinus

Here used for a cavity in the basisphenoid detectable in the dried skull, without regard as to the nature of its lining, etc.

Sphenopalatine Foramen (Nasopalatine Foramen)

A foramen located in the rostroventral portion of the orbit, bordered at least in part by the palatine bone, transmitting a nerve from the sphenopalatine ganglion and the sphenopalatine artery. (Story, 1951, p. 512.)

Sphenorbital Fissure

See foramen lacerum anterius.

Stapedial Artery

See arteria stapedia.

Stapedius Muscle

A small skeletal muscle, innervated by the facial (VII) nerve, inserting upon the stapes and originating from the petrosal. (Schaeffer, 1942, p. 1233.)

Stylomastoid Foramen

A foramen for the exit of the facial (VII) nerve from the middle ear (and sometimes for the entrance of the stapedius muscle). See foramen stylomastoideum definitivum, foramen stylomastoideum primitivum. As here used it is a neutral term without prejudice as to whether a foramen lacerum primitivum or a foramen lacerum definitivum.

Suboptic Foramen

"The so-called suboptic foramen is situated in the orbitosphenoid shortly posterior to the orbitonasal (sphenopalatine) foramen. It leads to a transverse canal through the presphenoid, immediately posterior to the olfactory chamber, and carries a vein which connects the ophthalmic veins." (Butler, 1948, p. 454.)

Superior Petrosal Sinus

A venous sinus of the dura mater running along the superior margin of the petrous bone, grooving the latter (this groove, often roofed by a process of the squamosal, sometimes called the aqueduct of Verga). It connects the cavernous venous sinus with the transverse venous sinus. (Schaeffer, 1942, p. 713.)

Tegmen Tympani

A thin lamina of bone projecting laterally from the petrosal to form part of the roof of the middle ear. (Schaeffer, 1942, p. 147.)

Tensor Tympani

A skeletal muscle, innervated by the otic ganglion of the trigeminal (V) nerve, inserted on the malleus and arising from the alisphenoid or (Soricidae, Solenodontidae) the membrane of the pyriform fenestra. (Schaeffer, 1942, p. 1233.)

Transverse Canal

A venous canal that pierces the basisphenoid to extend from one side of the skull to the other. (Gregory, 1910, p. 431.) See foramen Vesalii.

Tympanic

When used as a noun here, the tympanic (ectotympanic) bone, a bone supporting the eardrum. As an adjective, here used to mean having to do with the middle-ear cavity.

Tympanic Cavity

The middle-ear cavity.

Tympanic Process of Petrosal

A process of the petrosal (or periotic) bone in the wall of the middle-ear cavity. It is possible that in some mammals an apparent tympanic process of the petrosal is actually an entotympanic fused to the petrosal. But in the Macroscelididae the tympanic process of the petrosal and entotympanic co-exist, disproving homology in this case, at least. (See Van der Klaauw, 1931, pp. 285–289.)

Tympanohyal

". . . The most cranial element of the hyoid bar, which in general, especially in many of the lower mammals, forms a little process of the hinder part of the crista facialis petrosi, where it is connected with the periotic and forms the so-called processus hyoideus." (Van der Klaauw, 1931, p. 239.)

Ventral Facet of Occipital Condyle

The name given here to the portion of the occipital condyle ventral and anterior to the foramen magnum and facing ventrad.

Vertical Lamina of Palatine

As defined here, the portion of the palatine forming part of the lateral wall of the choanal passage. Essentially equivalent to "perpendicular process" (as used by Schaeffer, Sisson, and others), but restricted to the portion lateral to the choanal passage, ventral to the ethmoid. See orbital wing.

Vidian Branch of Arteria Promontorii, Vidian Artery

The name given here to the branch of the arteria promontorii that runs forward to enter the pterygoid canal along with the great superficial petrosal nerve. In the Lipotyphla, as well as the Leptictidae, this artery passes through the basisphenoid (or, perhaps, between basisphenoid and alisphenoid) to emerge in the cranial cavity, lateral to the pituitary fossa. To this extent it is like the main carotid of marsupials and therapsid reptiles, but the significance of this is uncertain.

Vidian Canal

The pterygoid canal.

Vidian Foramen

Here used to mean the posterior orifice of the pterygoid canal, for the escape of the Vidian nerve and artery from the middle ear.

Vidian Nerve

A nerve, also called the nerve of the pterygoid canal, formed by union of the great superficial petrosal nerve and great deep petrosal nerve, running forward from the middle ear through the pterygoid (Vidian) canal to the sphenopalatine ganglion (Schaeffer, 1942, p. 1069). It thus represents, in essence, the palatine branch of VII plus a sympathetic component.

ABBREVIATIONS

For Text Figures

AC, alisphenoid canal
ALGR, groove representing alisphenoid canal
AP, arteria promontorii
AS, stapedial artery (arteria stapedia)
AV, aquaeductus vestibuli
CBR, caudo-buccal root (on teeth); alveolus for caudo-buccal root (on maxillary sockets)
CC, posterior orifice of condyloid canal
CF, carotid foramen
CG, carotid groove
CP, line of intersection of orbital wall with cribriform plate
CR, caudal root (on teeth); alveolus for caudal root (on dentary sockets)
DC, orifice of dental canal
ECF, external capitular facet
EF, ethmoidal foramen or foramina
EH, tympanohyal
EM, extension of maxilla along pyterygoid crest
ENT, entotympanic
EOFA, external orifice of Fallopian aqueduct

EP, entoglenoid process
ETR, epitympanic recess
EV, area of origin of erector vibrissorum muscle
FLA, foramen lacerum anterius (sphenorbital fissure)
FLP, foramen lacerum posterius
FO, fenestra ovalis
FP, groove for Folian process of malleus
FPM, Folian process of malleus
FR, fenestra rotunda
FSA, foramen for stapedial artery
FSM, fossa for stapedius muscle
GCT, groove for chorda tympani
GF, glenoid fossa
HF, hypoglossal foramen
HSC, sheath of horizontal semicircular canal
IAM, internal auditory meatus
IC, anterior orifice of infraorbital canal
ICA, internal carotid artery
IPS, exposure of inferior petrosal sinus
IRC, interradicular crest of Butler (on teeth); groove for interradicular crest of Butler (on alveoli)
LF, lacrimal foramen
LFC, lateral facet of occipital condyle
LLS, scar for origin of levator labii superioris muscle
LR, lingual root (on teeth); alveolus for lingual root (on maxillary sockets)
M, mastoid
MA, malleus
MR, exposure of molar root
NC, nuchal crest
NF, foramen for persistent notochord
OC, occipital condyle
OF, foramen ovale
OP, optic foramen
OTT, alisphenoid origin of tensor tympani muscle
PAN, passage for auricular nerve
PCF, postglenoid capitular facet
PE, facet for tympanic process of petrosal
PF, parafloccular (subarcuate) fossa
PGF, postglenoid foramen
PGP, postglenoid process
PH, hamular process of pterygoid
POC, preotic crest
PP, paroccipital process
PPC, dorsal orifice of posterior palatine canal
PPF, postparietal foramen
PR, promontorium
PT, pterygoid lamina
PTP, posttympanic process (of squamosal)
PY, pyriform fenestra
RBR, rostro-buccal root (on teeth); alveolus for rostro-buccal root (on maxillary sockets)
RI, ramus inferior of stapedial artery; also foramen or groove for ramus inferior of stapedial artery
RM, recessus meatus
RR, rostral root (on teeth); alveolus for rostral root (on dentary sockets)
RS, ramus superior of stapedial artery
S, sagittal crest
SC, anterior orifice of sinus canal
SF, sphenopalatine foramen
SMF, foramen stylomastoideum
SP, anteromesial spine of tympanic
SPN, foramen for great superficial petrosal nerve
ST, stapes
TC, orifice of transverse canal (foramen Vesalii)
TM, limit of anterior extent of temporal muscle
TP, tympanic process of petromastoid
TY, tympanic bone
TYB, tympanic wing of basisphenoid, or vestige of same
VF, Vidian foramen (posterior orifice of Vidian canal)
VFC, ventral facet of occipital condyle
VR, Vidian ramus of arteria promontorii
XS, fenestra in mastoid for origin of stapedius muscle
ZS, zygomatic process of squamosal

For Catalogues of Specimens

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U.S.N.M., United States National Museum

AN OUTLINE OF THE HISTORY OF CLASSIFICATION OF THE ANTILLEAN INSECTIVORES

1833

J. F. BRANDT DESCRIBES the Hispaniolan *Solenodon paradoxus* from a skin and imperfect skull (lacking occiput).

1834

Poey makes known the occurrence of *Solenodon* in Cuba (in a newspaper, "El Plantel").

1840

H. M. D. de Blainville figures the skull of *Solenodon* (after Brandt), placing *Solenodon* as a subgenus of *Sorex*, while making the tenrecs a subgenus *Centetes* of *Erinaceus*.

1851

Poey gives a detailed account of the Cuban *Solenodon*, believing it conspecific with the Hispaniolan species.

1864

Wilhelm Peters describes the anatomy of the Cuban *Solenodon* and recognizes it as a distinct species, *S. cubanus*. Peters divides the insectivores into two series, one with and one without an intestinal caecum. [The formal names Menotyphla and Lipotyphla for these series were later bestowed by Haeckel (1866)]. Peters places *Solenodon* in a group "Centetinae" of the series without caecum, along with the Malagasy tenrecs.

1866

Andrew Murray places *Solenodon* as a close relative of the shrews and denies tenrec relationships, basing his decision largely on external morphology.

1871

St. George Mivart, although placing the lately discovered *Potamogale* in a separate family, places *Solenodon* in the Centetidae with the tenrecs.

1872

Theodore Gill erects a superfamily Centetoidea with two families, Potamogalidae and Centetidae, the latter containing the Madagascar tenrecs and *Solenodon*. But *Solenodon* is segregated in a separate subfamily from the Malagasy forms.

1882–1890

Dobson elevates Gill's Solenodontinae to full family rank, giving detailed accounts of the soft anatomy and osteology of *Solenodon cubanus*. Dobson makes the primary separation of insectivores between zalambdodonts and dilambdodonts, placing the Solenodontidae, Centetidae (=Tenrecidae), Potamogalidae, and Chrysochloridae in the former division, the shrews, moles, erinaceids, and menotyphlans in the second. Dobson does not commit himself against Murray's view that *Solenodon* is related to the Soricidae, but holds that more evidence is needed in the question (Dobson did not complete his anatomical studies of the Soricidae). Dobson is impressed by resemblances of *Solenodon* to *Myogale* (=*Desmana*).

1903

Matthew describes two fragments of lower jaws from the Chadron of Montana as the new genera and species *Apternodus mediaevus* and *Micropternodus borealis*.

1907

Leche publishes a monographic study of the zalambdodonts, including *Solenodon* in that group, but noting considerable anatomical difference from the other zalambdodonts. Leche regards the zalambdodont dentition as primitive.

In this same year, A. H. Verrill rediscovers *Solenodon paradoxus* in Hispaniola, obtaining the third, fourth, and fifth known specimens (Brandt's type and a specimen donated to the British Museum being the first and second). Nelson also collects *Solenodon paradoxus* for the Museum of Comparative Zoology at Harvard College.

1908

J. A. Allen reports on these three specimens of *Solenodon paradoxus* obtained by Verrill, the first described specimens since

Brandt's type. Allen does not himself investigate the affinities of the genus *Solenodon*, saying merely that it is closest to the Madagascar tenrecs and is generally regarded as a survivor of an unknown ancient primitive type. He does, however, give a detailed comparison of the skull of *Solenodon paradoxus* with that of *S. cubanus*.

1909

Matthew presents a diagrammatic classification of the insectivores, presenting both the division into Menotyphla and Lipotyphla and the division into Dilambdodonta and Zalambdodonta, but without commitment as to which split is the more basic. Matthew brackets the Solenodontidae with the Centetidae, Potamogalidae, and Chrysochloridae.

1910

G. M. Allen publishes an extensive account of the osteology and soft anatomy of *Solenodon paradoxus*, making comparisons with Dobson's account of the anatomy of *S. cubanus*. Allen states that *Solenodon* is undoubtedly closest to *Centetes* (=*Tenrec*), but differs from it in many specialized features.

Gregory gives a detailed analysis of the osteology of *Solenodon paradoxus* and gives a good account of the basicranium. He accepts Leche's conclusions as to the relationship of *Solenodon* to the tenrecs, but stresses resemblances to the leptictids (it may be said here that these resemblances are largely based on misinterpretations of the leptictid skull based on damaged material). He agrees with Leche on the homology of the cusps in the zalambdodont molar, regarding the most projecting cusp as the protocone, rather than an amphicone, and the supposed protocone as a cingulum cusp. It is suggested that the Oligocene *Micropternodus* Matthew is a centetid and that *Apternodus* Matthew is a centetoid.

Matthew describes a damaged but nearly complete skull of *Apternodus*. He places the genus in a new subfamily, Apternodontinae, of the Centetidae, comparison being made particularly with *Ericulus*. Matthew concludes, on the basis of *Apternodus*, that the zalambdodont dentition did not arise from the tritubercular dentition, nor did the tritubercular molar arise from the zalambdodont molar, in agreement with Leche; but he differs from Leche in believing the soricid and talpid molar pattern derived from the tritubercular rather than the zalambdodont pattern. Although Matthew lists *Solenodon* as one of the zalambdodonts, he presents no comparison with *Apternodus*.

1913

Matthew describes a damaged skull, with jaws, from the Puerco of New Mexico as *Palaeoryctes puercensis*. He regards this new genus as a possible central type from which the Solenodontidae, Centetidae, Potamogalidae, and Chrysochloridae might be derived. On the basis of this new find, Matthew reverses his previous opinion and holds that the zalambdodont dentition is derived from the trituberculate molar pattern by fusion of paracone and metacone. He holds that the living zalambdodont families are not closely related, but connected by *Palaeoryctes*. *Solenodon* shows some special cranial resemblance to *Palaeoryctes*, but is quite different in dentition, according to Matthew.

1916

Anthony makes known the occurrence of an additional genus of West Indian insectivores, *Nesophontes*, based on sub-Recent material from a cave in Puerto Rico. This new species, *Nesophontes edithae*, appears to Anthony to have no close relatives, and to require a new family, Nesophontidae. However, it appears to show some relationship to the Soricidae. The zalambdodonts, including *Solenodon*, are dismissed from comparison because of dental differences.

1917

Winge places *Solenodon* in the Centetidae (equivalent to the zalambdodonts) in a subfamily Solenodontini, including also *Palaeoryctes* and *Apternodus*, distinguished from the other zalambdodonts by absence of the tympanic process of the basisphenoid. *Nesophontes* (known to Winge only through Anthony's paper) is placed in a special subfamily of the Talpidae, where it is regarded as the most primitive genus. (This work has been available to me in the English translation by G. M. Allen and E. Deichmann, and is cited in the bibliography as Winge, 1941.)

G. M. Allen describes an additional species

of *Nesophontes*, *N. micrus*, based on a jaw from a Cuban cave.

Peterson records *Nesophontes micrus* from a cave on the Isle of Pines.

1918

G. M. Allen describes additional material of *Nesophontes micrus* and gives arguments for considering *Nesophontes* and *Solenodon* related to the tenrecs. He denies close relationship of *Nesophontes* to the Soricidae.

Anthony presents a detailed account of the osteology and dentition of the Puerto Rican *Nesophontes edithae*. His opinions on relationships remain much as in 1916, but he does not deny possible zalambdodont affinities.

1919

Anthony presents a resume of cranial differences between *Nesophontes edithae* and *N. micrus*. He describes a new species of *Nesophontes*, *N. longirostris*, from a Cuban cave deposit.

1920

Gregory (1920b), reviewing the comparative anatomy of the lacrimal bone, notes that the skull of *Nesophontes* much resembles that of a young *Solenodon*, and Gregory speaks of *Nesophontes* as a primitive zalambdodont.

1925

Anthony publishes a review of Puerto Rican mammals, including *Nesophontes edithae*, and attempts to refute G. M. Allen's argument that *Nesophontes* is close to *Solenodon* by citing paleontological arguments for the antiquity of the zalambdodont tooth form, and by presenting evidence for close relationship of *Nesophontes* to the Soricidae.

Cabrera separates *Solenodon cubanus* generically as *Atopogale*.

1929

G. S. Miller, Jr., describes three species of *Nesophontes* from Hispaniola, *N. paramicrus*, *N. hypomicrus*, and *N. zamicrus*.

1931

Simpson presents a classification of the mammals, in which *Solenodon* is placed in the Tenrecoidea (a corrected name for the Centetoidea of previous authors), and *Nesophontes* is placed in the Nesophontidae of the Soricoidea. *Apternodus* is placed in the Apternodontidae and *Palaeoryctes* in the Palaeoryctidae, both families of Tenrecoidea. (Although "Apternodontidae" is credited to Matthew, Matthew proposed only the subfamily Apternodontinae, and Simpson is the author of the family name.)

1933

Schlaikjer presents a study of a nearly complete skull of *Apternodus* and concludes that the genus is closely related to *Solenodon*. He appears to be unaware that Winge had reached a similar conclusion 16 years previously. He suggests *Micropternodus* as an ancestral solenodontid. No mention is made of *Nesophontes*.

1934

Schlaikjer reëxamines the *Apternodus* skull described by Matthew in 1910 and adds important new morphological information, as well as correcting some errors.

1936

Scott and Jepsen retain family status for the Apternodontidae, noting that it is most closely related to the Solenodontidae and Tenrecidae. *Micropternodus* is included in the Solenodontidae "with some doubt," and a description by John Clark of a closely related new genus, *Clinodon*, is included [*Clinodon* (preoccupied) is later renamed *Clinopternodus* by Clark].

1937

Matthew (in a posthumous publication of a 1930 manuscript) refers the Solenodontidae to the Centetoidea, and the Nesophontidae (with a question mark) to the Erinaceoidea.

1940

Wislocki reports on a placenta of *Solenodon paradoxus*, finding the placenta quite different from that of Old World zalambdodonts and similar to that of Soricidae.

1945

Simpson presents a revised classification of the mammals, essentially similar (with respect to West Indian insectivores) to that he presented in 1931, but the family Apterno-

dontidae is reduced to a subfamily of the Solenodontidae, following Schlaikjer. The Oligocene North American genera *Clinopternodus* and *Micropternodus* are included in the Solenodontinae.

1954

Saban proposes a superfamily, Nesophontoidea, for *Nesophontes*. The Soricoidea, Chrysochloroidea, and Tenrecoidea of Simpson are grouped together as a soricomorph series, in contrast to erinaceiomorphs, but no special affinity between *Solenodon* and *Nesophontes* is suggested.

1956

Butler shows the naturalness of the Lipotyphla, recognizing the group as an order and dividing it into two suborders, Erinaceomorpha and Soricomorpha, the latter including the shrews, moles, chrysochlorids, tenrecs, and West Indian insectivores. Butler notes *Nesophontes* as being annectant between soricoids and tenrecoids.

Hough describes a new genus, *Oligoryctes*, from the North American Oligocene, related to *Apternodus*. She argues strongly against any special affinity between *Apternodus* and *Solenodon*.

NESOPHONTES AND *SOLENODON* COMPARED

General Form of the Skull

The general form of the skull is similar in *Nesophontes* and *Solenodon*. It is elongated and low, with a projecting rostrum that is constricted anterior to P^3, but expanded transversely in the molar region, so that the rostrum has a vase-like form as seen from above or below. The zygomatic arch is broadly interrupted and represented only by the outwardly directed zygomatic processes of the maxilla and squamosal. The small orbit is completely confluent with the temporal fossa, and there is no trace of a postorbital process. There is a slight anterior temporal constriction. The braincase is essentially tubular in form and relatively long posterior to the glenoid articulation. Posterior to the glenoid articulation, the lateral profiles of the braincase are slightly convergent posteriorly.

The interpterygoid fossa is narrow and elongate, flanked by simple pterygoid-laminae without ectopterygoid laminae. The hamular processes are obtusely triangular and are not drawn out into spines (or, in some specimens of *Solenodon*, have only minute vestiges of hamular spines). The auditory region is open ventrally, closed partially by the horizontal tympanic ring. The condyles are large and S-shaped, flanking a relatively very large foramen magnum (particularly large in *Nesophontes*). The occiput is overhung by the nuchal crest, the latter extending not upward, but backward in cantilever fashion, to extend the parietal area, but not to increase the occipital area to any notable extent. The nuchal crest is weakest in the small species of *Nesophontes* (e.g., *N. micrus*), stronger in the large *Nesophontes edithae* and juvenile *Solenodon*, and very strong in adult *Solenodon paradoxus*. From above the crest appears bi-

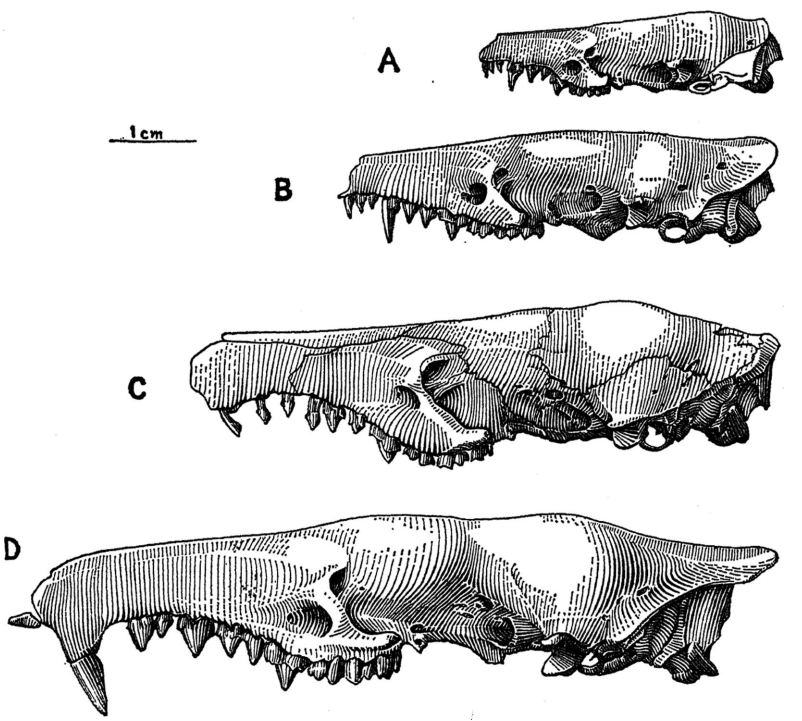

Fig. 1. Lateral views of the skull. A. *Nesophontes micrus*. B. *N. edithae*, (?) male. C. *Solenodon paradoxus*, juvenile. D. *S. paradoxus*, adult.

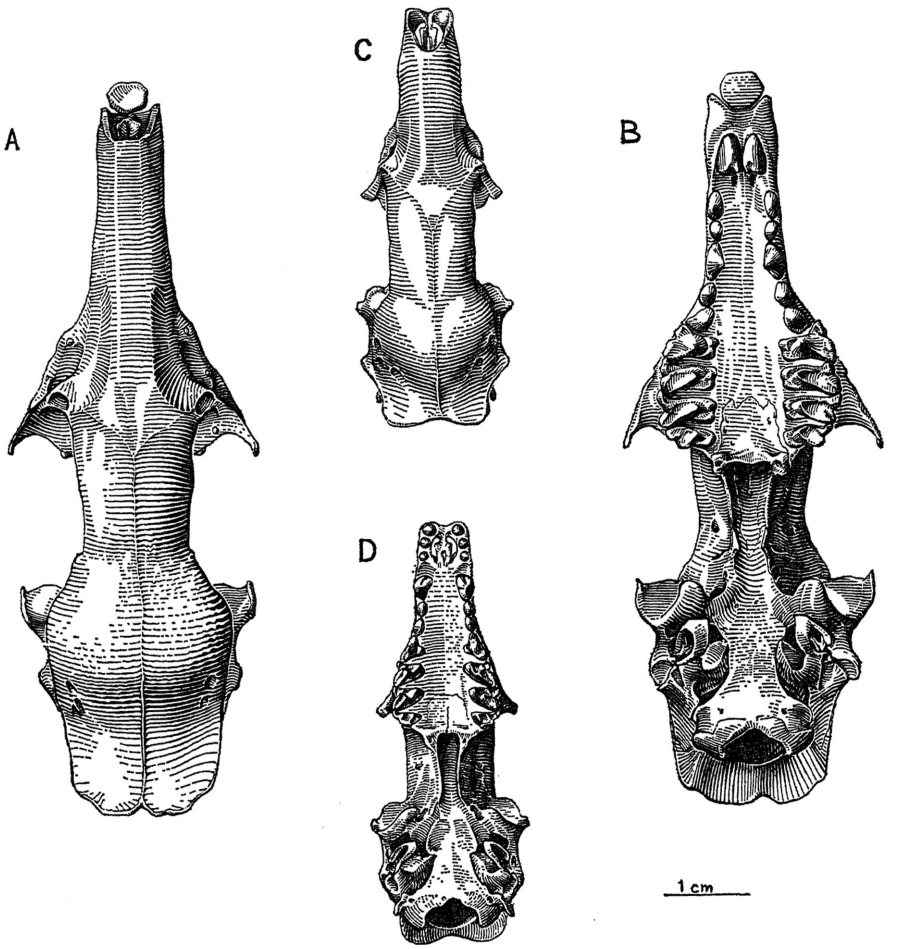

FIG. 2. Dorsal and ventral views of the skull of *Solenodon* and *Nesophontes*. A. *S. paradoxus*, dorsal view. B. Same, ventral view. C. *N. edithae*, (?) male, dorsal view. D. Same, ventral view.

lobate, as it is more produced laterally than sagittally. The mastoid is exposed laterally but not occipitally.

The sagittal crest is very weakly developed, except at its extreme posterior end, where it joins the nuchal crest. Anteriorly, the feeble sagittal crest divides into a pair of still feebler diagonal crests running towards the preorbital rim. The preorbital rim is sharp, without lacrimal tubercle, and bears the large lacrimal foramen. The lacrimal foramen opens diagonally backward and outward, but is essentially intraorbital in position. Just anterior and dorsal to the orbit there is a scar for the origin of the levator nasi superioris. The infraorbital canal is very short, with a narrow and strap-shaped lateral wall. In both genera, in spite of considerable difference in the proportions of the anterior teeth, the alveolar border of the rostrum has a similarly sinuous profile, descending posteriorly in a downwardly convex arc, but curving upward medially to be high and horizontal anteriorly.

The alveolar border of the dentary is nearly straight and horizontal in both genera, while the ventral border of the dentary is conspicuously convex downward. In both genera the horizontal ramus of the dentary is heavy, the coronoid process broad and in the form of a truncated triangle. The condyle is expanded transversely by inward extensions of its me-

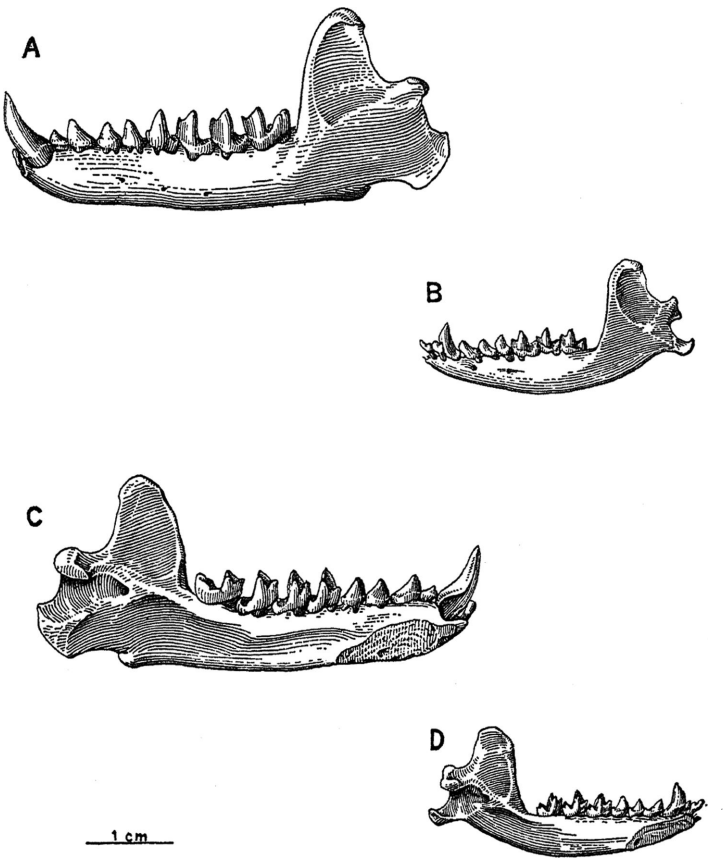

FIG. 3. Lower jaws of *Solenodon* and *Nesophontes*. A. *S. paradoxus*, lateral view. B. *N. edithae*, lateral view. C. *S. paradoxus*, mesial view. D. *N. edithae*, mesial view.

sial extremity and is approximately on the line of molar occlusion. The angular process is in the plane of the body of the mandible, but a crest on its ventral, mesial surface gives it the appearance of being weakly inflected.

But it is not the general conformation of the skull that argues most strongly for affinity between *Nesophontes* and *Solenodon*, but rather the agreement in detail of certain portions of the skull. These resemblances, to be discussed in detail in the following pages, concern: (1) the ear region; (2) the squamosodentary articulation; (3) the orbit and its associated foramina; (4) the scars for nasal muscles; (5) the teeth, which, although the structures that show the greatest difference between *Nesophontes* and *Solenodon*, nonetheless offer suggestive resemblances.

AUDITORY REGION

Nesophontes and *Solenodon* show great similarity in auditory structure, having a type of ear seen elsewhere only in the Soricidae and in marked contrast to the ear of other Lipotyphla. Chief characteristics of the ear found in the Soricidae, *Nesophontes*, and *Solenodon* are:

1. Basisphenoid with bullar wing vestigial or absent, not in contact with the tympanic. As a result, the tympanic cavity is largely open ventrally in the dried skull. In further consequence, the alisphenoid contribution to the roof of the middle ear is rather poorly distinguished from the basisphenoid.

2. The anterior portion of the petrosal (the portion bearing most of the origin of the tensor tympani in other insectivores) is absent, and the epitympanic wing of the ali-

sphenoid is reduced, a membrane replacing these normally bony structures. This has numerous consequences in changing the form of vascular canals through the auditory region.

TYMPANIC: This bone is similar in most respects in the two Antillean genera. In both genera the ring is incomplete posterolaterally, the gap being closed by the body of the malleus; in both, it bears an oblique groove across its anterolateral limb for the Folian process of the malleus; in both there is a prominent fossa on the internal surface representing a moderately well-developed recessus meatus. In both genera, the nearly horizontal tympanic is supported posteromedially by a strong tympanic process of the petrosal, while its anterolateral limb rests against the meatal surface of the squamosal (except where it is separated from the latter by the Folian process of the malleus), immediately lateral to the postglenoid foramen.

The tympanic is known for but one individual (A.M.N.H. No. 17108) of a single species (*N. edithae*) of *Nesophontes*. It shows the following differences from the tympanic of *Solenodon*: very weak development of the anteromesial spine, the ring being of much rounder and less angulate form; relatively shorter surface for attachment to the tympanic process of the petrosal; less dilated dorsal extremity of the anterolateral limb. [The description of the tympanic of *Nesophontes* given by Anthony (1925, p. 72) is based on A.M.N.H. No. 17108, but without allowance for a post-mortem displacement of the bone that is revealed by further cleaning.] The great rarity of tympanics among *Nesophontes* material suggests that in that genus the bone is never fused with the tympanic process of the petrosal. However, in *Solenodon* large skulls show such fusion, in spite of the contrary statement of G. M. Allen (1910, p. 34).

MUSCULAR FOSSAE: The peculiar modification of the area of origin of the tensor tympani, characteristic of *Solenodon*, *Nesophontes*, and the Soricidae, has been noted above. Because of the reduction of the petrosal, the

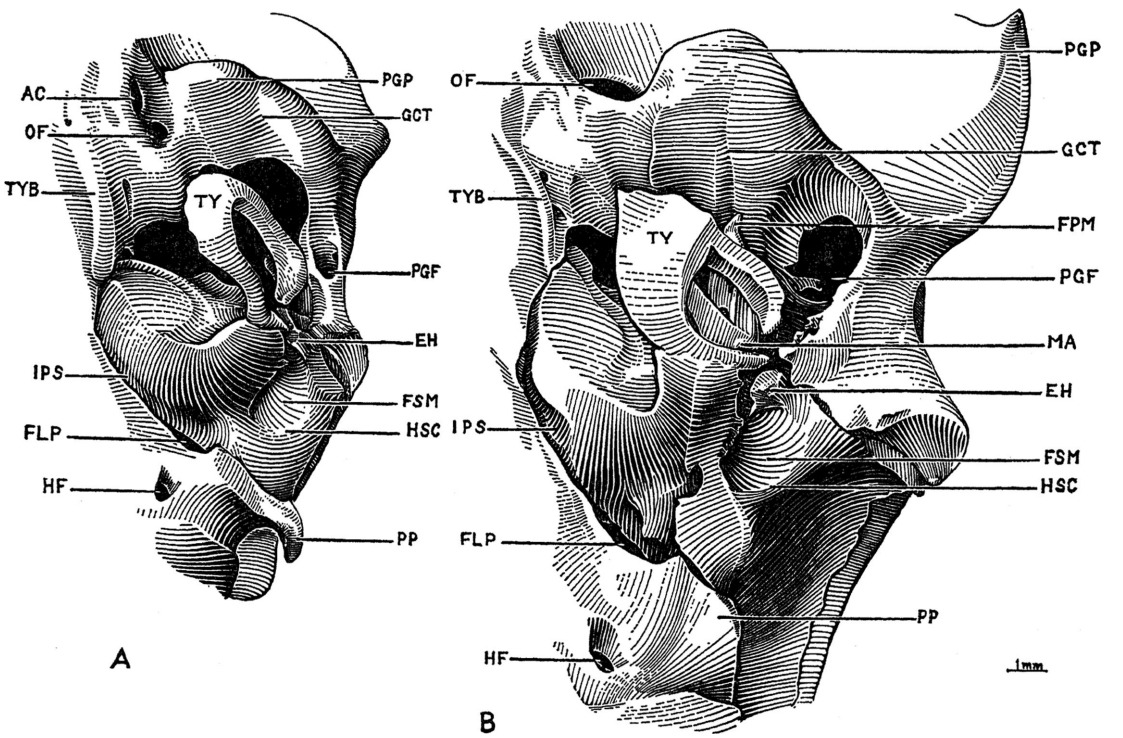

FIG. 4. Ventral view of the ear region of the skull. A. *Nesophontes edithae*. B. *Solenodon paradoxus*. The malleus (MA) has been omitted in A, but drawn in B. Abbreviations on page 129.

greater portion of the area of origin of the tensor tympani is membranous. However, the portion of the alisphenoid normally bearing the anterior part of the origin of the muscle is not entirely reduced, showing a semilunar scar for the tensor tympani, lateral to the groove for the Vidian branch of the arteria promentorii. The relatively shorter and wider proportions of the ear region in *Solenodon*, as compared with that in *Nesophontes*, affect the proportions of the vacuity in the fossa for the tensor tympani. In *Solenodon* the vacuity is relatively wider and shorter anteroposteriorly than in *Nesophontes* and does not extend so far anterolaterally.

The vacuity in the roof of the tympanic cavity of *Solenodon* was noticed by Gregory (1910, p. 247), who noted a vacuity similar to a foramen lacerum medium, but occluded in an adult skull by the tympanic roof. Specimens of *Solenodon paradoxus* with the muscles dried in place show this vacuity to be in the fossa for the muscle and only incidentally involved in arterial passage. The reference of Anthony (1925, p. 92) to "The wide separation of postglenoid process and periotic" as a resemblance between *Nesophontes* and the Soricidae appears to be an allusion to the vacuity in the muscular fossa. Grassé (1955, p. 1590) has noted that in soricids, "*la paroi dorsale de la cavité tympanique ne s'ossifie pas et une membrane conjonctive tendue entre le pétreux et l'alisphénoïde supplée à l'absence d'os.*" This appears to be the pyriform vacuity noted by Parker (1886) in *Sorex*, and in the following pages it is termed the pyriform fenestra.

The stapedius muscle originates on the mastoid just external and posterior to the stylomastoid foramen from a fossa bounded laterally and posteriorly by a swelling corresponding to the enclosed horizontal semicircular canal. It extends into the tympanic cavity through that foramen, there to insert upon the stapes. (This has been determined from a specimen of *Solenodon paradoxus* with the muscle dried in place.) *Nesophontes* has a nearly identical form of the stylomastoid region to that seen in *Solenodon* and presumably had a similar stapedius muscle.

VENOUS CANALS: The suppression of the anterior portion of the petrosal causes the postglenoid foramen to open directly into the

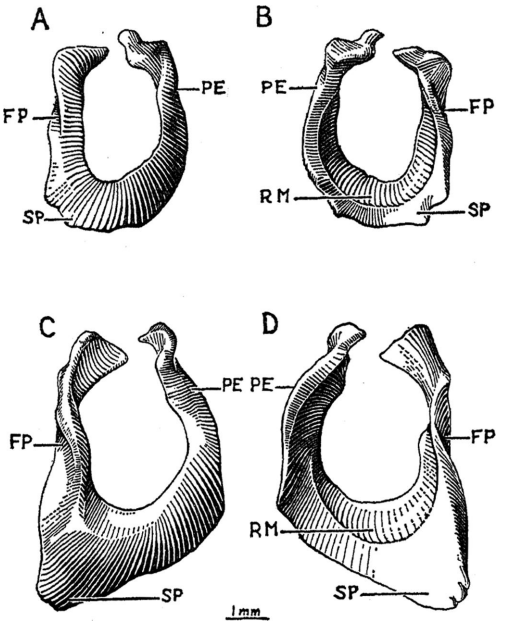

FIG. 5. Left tympanic bones of *Nesophontes* and *Solenodon*. A. *N. edithae*, external view. B. Same, internal view. C. *S. paradoxus*, external view. D. Same, internal view. Abbreviations on page 129.

cranial cavity, rather than into a bony canal between the squamosal and petrosal, the superior petrosal sinus being exposed intracranially. As in other Lipotyphla, the foramen is actually lateral to the parasagittal plane of the postglenoid process, rather than on or internal to that plane as in most mammals.

As in other lipotyphlan insectivores, the inferior petrosal sinus of *Nesophontes* and *Solenodon* is exposed ventrally, owing to the failure of the petrosal and basioccipital to form a suture beneath the sinus immediately anterior to the jugular (posterior lacerate) foramen. This exposure extends forward from the jugular foramen, with which it is continuous, approximately to the level of the basioccipital-basisphenoid suture.

ARTERIAL CIRCULATION: The course of arteries through the ear of *Solenodon* has been determined from specimens with the arteries dried in place. Because the arteries leave their imprint as distinct grooves, it has been possible to determine their course in *Nesophontes* as well. The pattern is virtually identical in the two genera and does not differ fun-

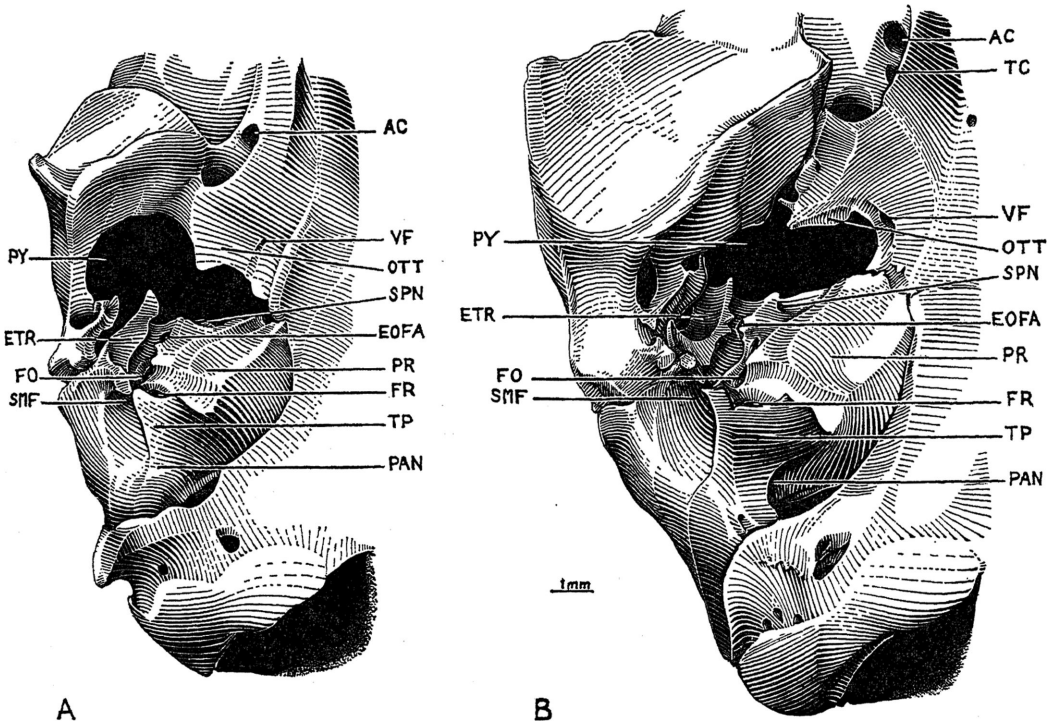

FIG. 6. Ventral view of ear region. A. *Nesophontes edithae*. B. *Solenodon paradoxus*. The tympanic and auditory ossicles are removed. B represents a juvenile with sutures open. Abbreviations on page 129.

damentally from the usual lipotyphlan pattern, as shown, for example, in *Erinaceus* (see Butler, 1948, p. 455).

The internal carotid excavates a groove extending diagonally across the promontorium, its course slanting forward and laterad. At about the center of the promontorium, the internal carotid divides into a mesial and a lateral branch.

The mesial branch (arteria promontorii) extends forward and mesiad across the sloping anterior surface of the promontorium to the anterior border of the petrosal (edge of the pyriform fenestra), at the mesial border of the tympanic cavity. Here the arteria promontorii divides into two branches. One branch enters the cranial chamber. The other, much smaller, is the Vidian artery, and runs forward to traverse a short groove in the alisphenoid part of the tympanic roof to enter a foramen (posterior orifice of pterygoid canal) at the anteromesial corner of the tympanic region.

The lateral branch of the internal carotid is the stapedial artery and extends forward and laterad across the lateral face of the promontorium to pass between the crura of the stapes. (Before passing through the stapes the artery, in *Solenodon* at least, gives off a small twig to foramina in the region of the stylomastoid foramen. Similarly placed foramina in *Nesophontes* suggest the presence of a corresponding branch of the stapedial artery.)

The stapedial artery divides into two branches, a ramus superior passing into the cranial chamber at the posterolateral corner of the pyriform fenestra to become the middle meningeal artery, and a large ramus inferior traversing a groove on the posterior surface of the (combined) preotic crest and postglenoid process, immediately medial to the groove for the chorda tympani.

The chief peculiarity of the stapedial arterial circulation is that the ramus superior does not make a long passage through the petrous

bone. Instead, as a consequence of the reduction of the anterior portion of the petrous bone, the stapedial artery is exposed.

PASSAGES FOR NERVES: The main facial nerve has been observed in one *Solenodon*, but not its branches; but its course may be assumed from the foramina in the petrosal. There appear to be no differences between *Nesophontes* and *Solenodon* in the course of the facial nerve.

The main trunk of the facial passes through a short and simply arched Fallopian aqueduct. The mesial opening of the aqueduct shares a fossa of the petrous bone with the internal auditory meatus. The external orifice of the aqueduct is somewhat variable in its position and may be either directly dorsal to the fenestra ovalis or more anteriorly located. In either case, the orifice opens into a sharply defined groove on the ventral (external) surface of the tegmen tympani. This groove leads backward to the stylomastoid foramen and conducts the facial nerve to that foramen. The anterior part of the groove is occupied by the tendon of the tensor tympani.

Just before opening externally, the Fallopian aqueduct gives off a canal that opens into the pyriform fenestra near the base of the promontorium. The anterior orifice of this canal, which is undoubtedly for the great superficial petrosal nerve, is flanked laterally by a short spine of the petrous bone. In *Solenodon* the anterior orifice of this canal is somewhat more ventral and exposed than it is in *Nesophontes*.

In both genera, there is a groove on the rear of the postglenoid process, corresponding to the position of a line continuing the Folian process of the malleus. This would appear to accommodate the chorda tympani, a nerve that accompanies the Folian process.

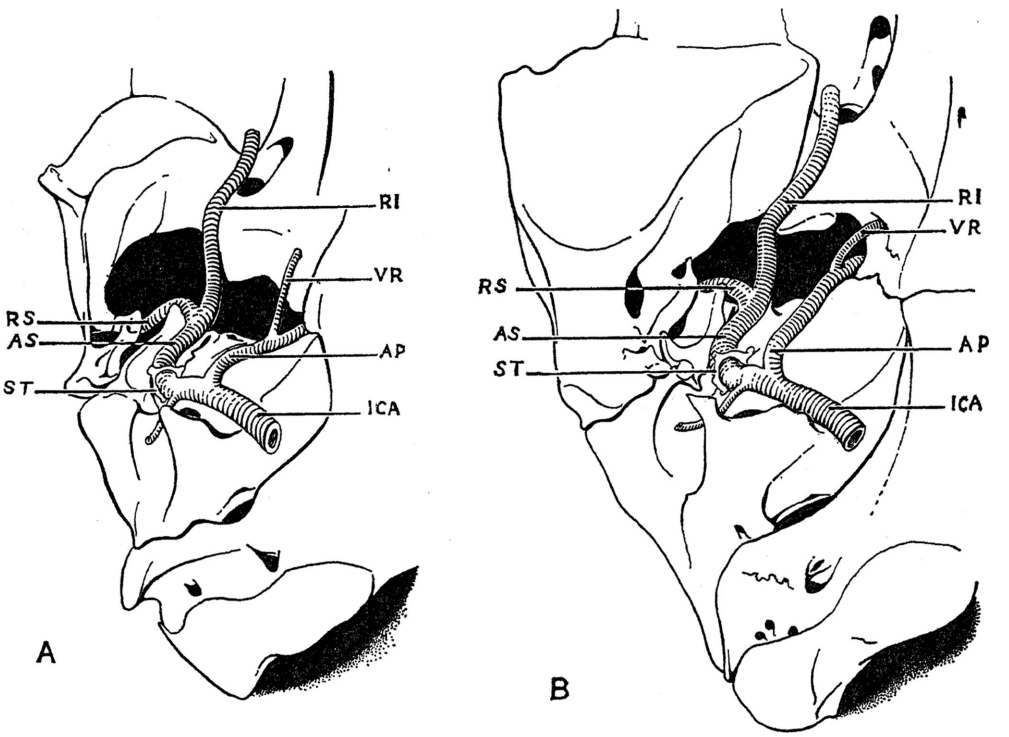

FIG. 7. Right middle-ear region, tympanic removed. A. *Nesophontes edithae*. B. *Solenodon paradoxus* (juvenile). The carotid circulation of *Solenodon* is based on specimens with the arteries dried in place; that of *Nesophontes* is restored from the grooves and foramina of the bones. Abbreviations on page 129.

In *Solenodon* the Folian process is pierced by the chorda tympani, as in most Lipotyphla. In available specimens of *Nesophontes*, the malleus is too broken for the presence or absence of a foramen for the chorda to be determined.

Solenodon differs from *Nesophontes* in having the groove for the auricular nerve converted into a closed canal by a bridge of bone.

SQUAMOSAL: In both genera, the squamosal makes virtually no contribution to the roof of the tympanic cavity. Its only contribution is to form the outer half of the very small epitympanic recess (attic). It is separated from the epitympanic wing of the alisphenoid by the pyriform fenestra.

TYMPANOHYAL: Although completely fused to the petromastoid, a short cylindrical process forming the lateral border of the stylomastoid foramen appears to represent the tympanohyal. A longitudinally oriented crest of bone (possibly the posterior *Chordafortsatz*) runs from the tympanohyal to the border of the pyriform fenestra. This crest, which is stronger in *Solenodon* than in *Nesophontes*, divides the more lateral epitympanic recess from the more mesial groove for the facial nerve.

BASISPHENOID: As in the Soricidae, but not as in other lipotyphlans, *Solenodon* and *Nesophontes* lack a bullar wing of the basisphenoid. A low blunt ridge mesial to the groove for the Vidian artery may represent this wing in the Antillean genera, but it does not even approach the tympanic bone and, rather than being a thin shell of bone, contains spaces of the sphenoid sinuses.

PETROMASTOID: In both genera the petromastoid is provided with a tympanic process that supports the tympanic and conceals the fenestra rotunda. This process contains vacuoles apparently continuous with the mastoid cellulae. The tympanic process forms the mesial border of the stylomastoid foramen.

The fenestra rotunda, as in other Lipotyphla, opens into a pit behind the promontorium. This pit is, in turn, roofed over by the tympanic process.

Dorsal to the fenestra rotunda, deep within the posterior lacerate (jugular) foramen, is a pit in the petromastoid ending in a very small (*Solenodon*) or moderate-sized (*Nesophontes*) foramen into the cochlea, the aquaeductus vestibuli.

The fenestra ovalis is almost rectangular and faces directly laterally.

SQUAMOSO-DENTARY ARTICULATION

The glenoid articulation of *Solenodon* is very similar to that of *Nesophontes*, both genera showing a stage of complexity intermediate between that of the Soricidae and that of other lipotyphlans. As in all Lipotyphla except the Soricidae, the condyle of the dentary is single; however, the capitular facets are divided, as in the Soricidae but not as in other mammals. (The capitular surfaces are distinguished by texture in cleaned skulls, and most easily revealed by first being rubbed with a soft lead pencil, then being rubbed with the finger tip.)

On specimens of *Solenodon paradoxus* with the glenoid articular apparatus dried in place, two separate ovoid spots of cartilage can be seen on the glenoid surface of the squamosal. One is on the external portion of the glenoid fossa (the portion of the fossa borne by the vestige of the zygomatic portion of the squamosal); this, the external capitular facet, faces directly ventrad. The other capitular facet lies more mesially, on the projecting postglenoid process; this, the postglenoid capitular facet, faces forward and dorsad. The external and postglenoid capitular facets are quite separate on the squamosal.

On the condyle of the dentary there are corresponding facets. The external facet lies on the most external portion of the condyle, in the plane of the ascending dentary ramus; this facet faces dorsad. The postglenoid facet is borne on a pointed, mesially directed process of the condyle, well internal to the plane of the ascending ramus. This facet is semicylindrical in form and faces backward and ventrad. The two facets are joined on the dentary by a narrow bridge, running from the most mesial portion of the external facet to the midpoint of the anterior border of the postglenoid facet.

The facets in *Nesophontes* are similar to those of *Solenodon*, save that the postglenoid facet of the dentary is relatively broader.

In both genera the glenoid articulation is relatively very broad, the width of the den-

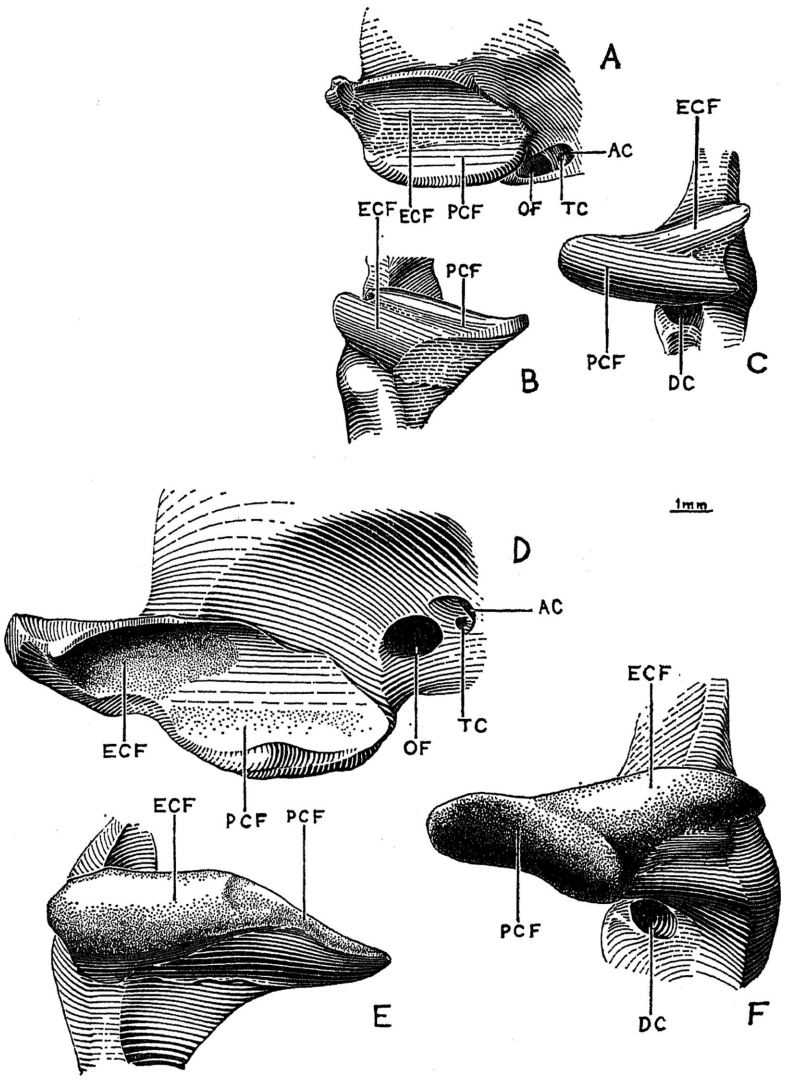

FIG. 8. Right squamoso-dentary articulation of *Nesophontes* and *Solenodon*. A. *N. edithae*, glenoid fossa. B. Same, dorsal view of dentary condyle. C. Same, condyle from behind. D. *S. paradoxus*, glenoid fossa. E. Same, dorsal view of dentary condyle. F. Same, condyle from behind. The capitular cartilages are represented in D, E, and F by stippling. In A, B, and C only the texture of the bone is represented. Abbreviations on page 129.

tary condyle exceeding the bucco-lingual diameter of the upper molars. The glenoid fossa is directed forward in both genera. In *Solenodon* the postglenoid process has a moderate ventrad inclination, as well as a rostrad direction, but in *Nesophontes* the process is directed almost straight forward.

In both genera the postglenoid process shows the peculiarities of the Lipotyphla not seen in most mammals, namely:

1. The process is located more mesially than in most mammals, internal to the parasagittal plane of the postglenoid foramen, rather than external to that plane. As a con-

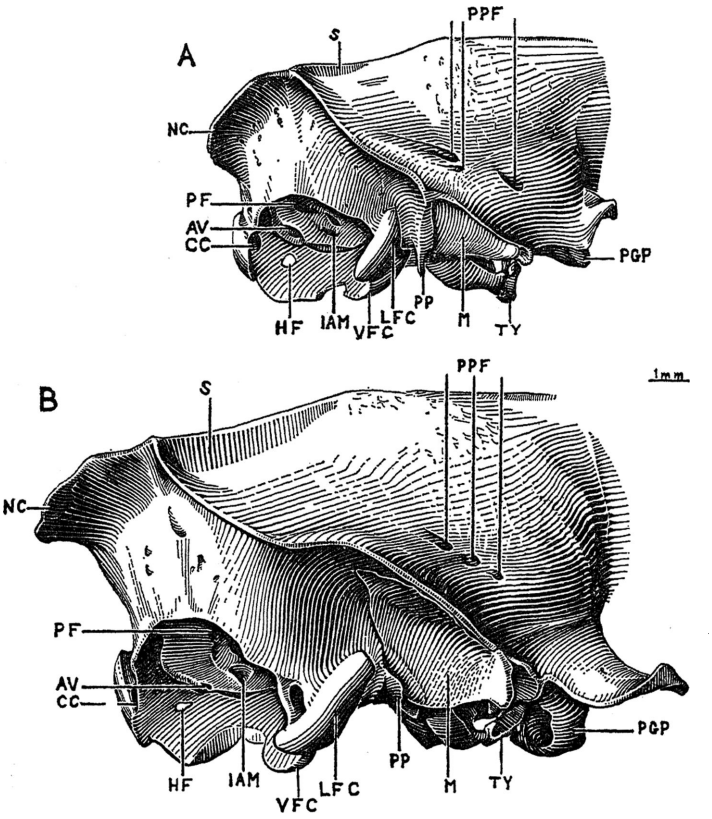

FIG. 9. Three-quarter view of the occiput. A. *Nesophontes edithae*. B. *Solonodon paradoxus*. Abbreviations on page 129.

sequence, the entire postglenoid process lies on the ventral surface of the braincase proper, none of the process being carried lateral to the braincase on the zygomatic arch. A further consequence is the posterior exposure of most of the lateral portion of the dentary condyle when the latter is articulated.

2. The postglenoid process is not set off from the preotic crest by a deep emargination for the chorda tympani (and, in the embryo, Meckel's cartilage), as it is in most mammals, but is continuous with the preotic crest of the alisphenoid, except for a small notch for the ramus inferior of the stapedial artery.

Nesophontes differs from *Solenodon* in the position of the glenoid fossa relative to the foramen ovale. In *Solenodon* the fossa lies slightly behind the foramen ovale, in the normal position. But in *Nesophontes* the fossa is brought forward anterior to the foramen ovale, so that the latter is sunk in a slight recess.

OCCIPITAL REGION

In both *Nesophontes* and *Solenodon* the nuchal crest is directed backward, rather than upward, to overhang the occipital region. Thus, the crest materially increases the parietal area (and, consequently, the origin of the temporalis muscle) without noticeably increasing the area of the inion for the insertion of the occipital musculature.

In both genera, the occiput is relatively narrow as compared with the rest of the braincase, being conspicuously narrower than the braincase across the auditory openings. The inion is formed entirely by the occipital bones, without contribution from the mastoid. [The obliteration of other sutures makes it impossible to determine in *Nesophontes*

whether or not the parietal, interparietal, or squamosal reaches the inion; but in the nestling *Solenodon paradoxus* (A.M.N.H.:M. No. 28272) it may be seen that all these elements fail to reach the border of the occiput; no tabular element is present.] As might be expected in the absence of the mastoid from the occipital surface, there is no postmastoid foramen on the occiput, but in the nestling *Solenodon* there is a small foramen on the lateral mastoid surface that is possibly homologous with the postmastoid foramen.

As noted in the account of the general appearance of the skull, absolute size appears to affect the proportionate development of the nuchal crest. It is best developed in large *Solenodon paradoxus* skulls, and nearly as well developed in large (?male) skulls of *Nesophontes edithae*, but much less developed in the small (?female) skulls of *N. edithae* and even feebler in the still smaller skull of *N. micrus*.

Always, the nuchal crest is bilobate, being divided by a slight median emargination into a pair of rounded wings. As a consequence, when viewed from behind, the occiput is slightly lower on the midline than just lateral to the sagittal plane, and the inion is essentially rectangular.

Solenodon differs from *Nesophontes* in the degree of development of the paroccipital process. In *Nesophontes* the process exists as a freely projecting spine forming the ventral extremity of a raised crest of the occipital immediately behind the mastoid. In *Solenodon* the process itself is absent, only the crest behind the mastoid remaining. But *Nesophontes micrus* is somewhat intermediate between *N. edithae* and *Solenodon* in this respect, for while the free process is present, it is minute.

In both *Solenodon* and *Nesophontes* the foramen magnum is relatively very large and of conspicuously greater transverse than vertical diameter. Its width is approximately two-thirds of the width across the condyles.

Both genera show the form of occipital condyle usual in primitive placentals: There are two facets, one ventral and anterior to the foramen magnum and another lateral to the foramen magnum and facing backward from its position on the inion; the two facets are joined by a narrowed isthmus of bone. In neither genus does the lateral facet extend upward to the level of the dorsal border of the foramen magnum, and in both genera the condyles are transversely oriented.

Both genera are characterized by a canal running longitudinally through the substance of the occipital bone medial to the condyle. The posterior orifice of this canal (presumably the venous condyloid canal) lies medial to the lateral facet of the occipital condyle just external (*Solenodon*) or just internal (*Nesophontes*) to the margin of the foramen magnum. The anterior orifices are several. One, the main anterior orifice, opens intracranially, just posterior to the posterior lacerate foramen. The position of the subsidiary anterior orifice is individually variable. It may open into the hypoglossal foramen, as in *Solenodon paradoxus* A.M.N.H.:M. No. 77752) and *Nesophontes edithae* A.M.N.H. No. 17096), or it may open independently anterior to the condyle lateral to the hypoglossal foramen, as in *Nesophontes edithae* (A.M.N.H. No. 55032). A single individual may have one type of subsidiary orifice on one side and the other type on the opposite side, as in *Nesophontes edithae* (A.M.N.H. No. 17655), or may possess both subsidiary anterior orifices on each side, as in *Solenodon paradoxus* (A.M.N.H.:M. No. 28272).

Orbital Region

Both *Solenodon* and *Nesophontes* have the orbit and temporal fossa completely confluent and relatively shallow. There is no postorbital process or frontal overhang, so that the orbit is not defined dorsally. The cribriform plate in both genera is very obliquely placed, at an angle of about 45 degrees, transecting the orbitotemporal fossa along a line marked externally by a slight concavity that becomes a distinct orbitotemporal constriction dorsally. The ventralmost portion of the cribriform plate extends slightly farther posteriorly in *Nesophontes* than in *Solenodon*.

It is impossible to determine the arrangement of sutures in the orbital region in *Nesophontes*, because only individuals with the sutures closed are known for that genus. The foramina are very similar to those of *Solenodon* in form and arrangement.

Lacrimal Foramen: This is a very large

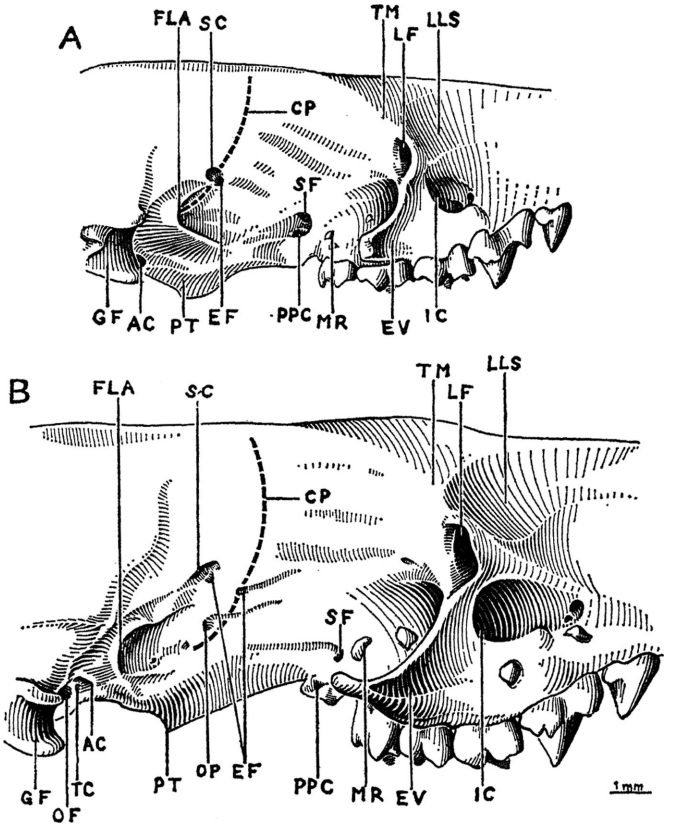

FIG. 10. Orbital region. A. *Nesophontes edithae*. B. *Solenodon paradoxus*. Abbreviations on page 129.

and conspicuous foramen, identical in form in the two genera. It lies essentially on the antorbital rim, neither inside nor outside the orbit, facing posterolaterally. The lacrimal canal is straight, running dorsal to the infraorbital canal, and expanded in trumpet-like fashion posteriorly to form the foramen. As in other Lipotyphla there is no indication of a lacrimal tubercle.

INFRAORBITAL CANAL: Identical in the two genera, this canal is notable for its large caliber and great brevity. It is confined to the maxilla above the second molar and is nearly circular in section. Passing between the lingual and buccal roots of the upper molars, the walls of the canal are perforated to reveal the apices of the molar roots. The canal opens anteriorly into a depression on the side of the maxilla; this fossa contains a small foramen leading into the nasal chamber.

SPHENOPALATINE FORAMEN: This is a relatively small foramen, identical in the two genera. It is located behind the last molar just dorsal to the orbital opening of the posterior palatine canal. Although it may share a shallow fossa with the last-named foramen, it is quite separate from it and forms no common canal with the posterior palatine canal. In neither genus is the sphenopalatine foramen connected by a trench with the foramen lacerum anterius.

POSTERIOR PALATINE CANAL: This foramen has a characteristic form and is similar in the two genera. It is bored vertically, and forked, with a single dorsal (orbital) opening, and two ventral (palatal) openings, one anterior and one posterior to the postpalatine torus. In the nestling *Solenodon* the postpalatine torus is unossified, and the posterior rim of the canal similarly defective, so that the posterior palatine canal is a simple notch in the rear border of the palatal surface of the

palatine. The next stage in development appears to be represented by a skull of *Solenodon paradoxus*, with many of the sutures still visible under magnification; here the rim of the canal is complete, but the lack of ossification of the postpalatine torus leaves the foramen undivided. The furcation of the canal would thus appear to be the result of the great lateral extent of the postpalatine torus.

SINUS CANAL: This foramen transmits the middle meningeal artery to its juncture with the ophthalmic artery, and the ophthalmic vein to the superior petrosal sinus. As in insectivores generally, it is of large size, and in both genera its opening is compound and closely approximated to the most dorsal of the ethmoidal foramina.

ETHMOIDAL FORAMINA: In both genera these foramina are several, a variable number of small foramina lying in the region of the optic foramen and supplying the ventralmost turbinate scrolls. But the most conspicuous ethmoidal foramen is the most dorsal, placed immediately anterior to the opening of the sinus canal; indeed, at first glance this foramen might appear to be a part of the sinus canal, as often it shares a fossa with that foramen.

OPTIC FORAMEN: This foramen is small but present in both genera. *Solenodon* differs from *Nesophontes* in the more anterior position of the foramen, so that it is exposed laterally; in *Nesophontes* the foramen is concealed laterally by the hood-like, lateral wall of the foramen lacerum anterius. This difference appears to be the result of the greater backward extent of the ventral portion of the cribriform plate in *Nesophontes*, forcing the optic foramen backward.

FORAMEN LACERUM ANTERIUS: This foramen, transmitting both the first and second divisions of the fifth nerve, has the form characteristic of insectivores, being hooded laterally by anterior extension of the alisphenoid.

ALISPHENOID CANAL: Both genera show the extreme case of the lipotyphlan type of alisphenoid canal. In lipotyphlans the mesial wall of the canal is greatly shortened by a slit-like, backward extension of the foramen lacerum anterius. In *Solenodon* and *Nesophontes* the mesial wall is altogether absent, so that the canal is indicated only by its circular posterior orifice which leads directly into the cranial cavity.

FORAMEN OVALE: This foramen is immediately mesial to the glenoid fossa and longitudinally ovoid. It is close behind the posterior orifice of the alisphenoid canal. In *Nesophontes* the foramen is more posteriorly located than in *Solenodon*, distinctly behind the glenoid fossa.

TRANSVERSE CANAL: In both *Nesophontes* and *Solenodon* a small foramen lies in the bony separation between the foramen ovale and posterior orifice of the alisphenoid canal. This foramen leads into the sinus contained in the basisphenoid and would appear to be the external orifice of a transverse (venous) canal, being so identified by Gregory (1910). The foramen is conspicuously larger in the nestling *Solenodon* than in the adults of *Solenodon* and *Nesophontes*.

SCARS FOR SNOUT MUSCLES

As indicated by Butler (1956), the area of origin of the muscles moving the proboscis is of considerable taxonomic value in the Lipotyphla. The scar for the levator labii superioris proprius in both *Solenodon* and *Nesophontes* is located on the side of the rostrum, anterodorsal to the orbit, the scars of the opposite sides being well separated.

(This is an arrangement most closely approximated in the Erinaceidae. In the Soricidae the muscle originates from near the midline on the dorsal surface of the skull, behind the orbit; in Old World "zalambdodonts" the muscle originates from the temporal fossa, beneath the temporalis; in talpids, the muscle originates from the zygoma. The two Antillean genera differ from the erinaceids in the failure of the muscle to extend dorsal to the orbit.)

The erector vibrissorum portion of the levator labii superioris arises from a scar on the base of the zygomatic process of the maxilla.

No differences between *Nesophontes* and *Solenodon* have been detected in the origin of the levator labii superioris.

DENTITION

It is on the basis of the dentition that *Solenodon* and *Nesophontes* have been separated widely in classifications of the Insectivora.

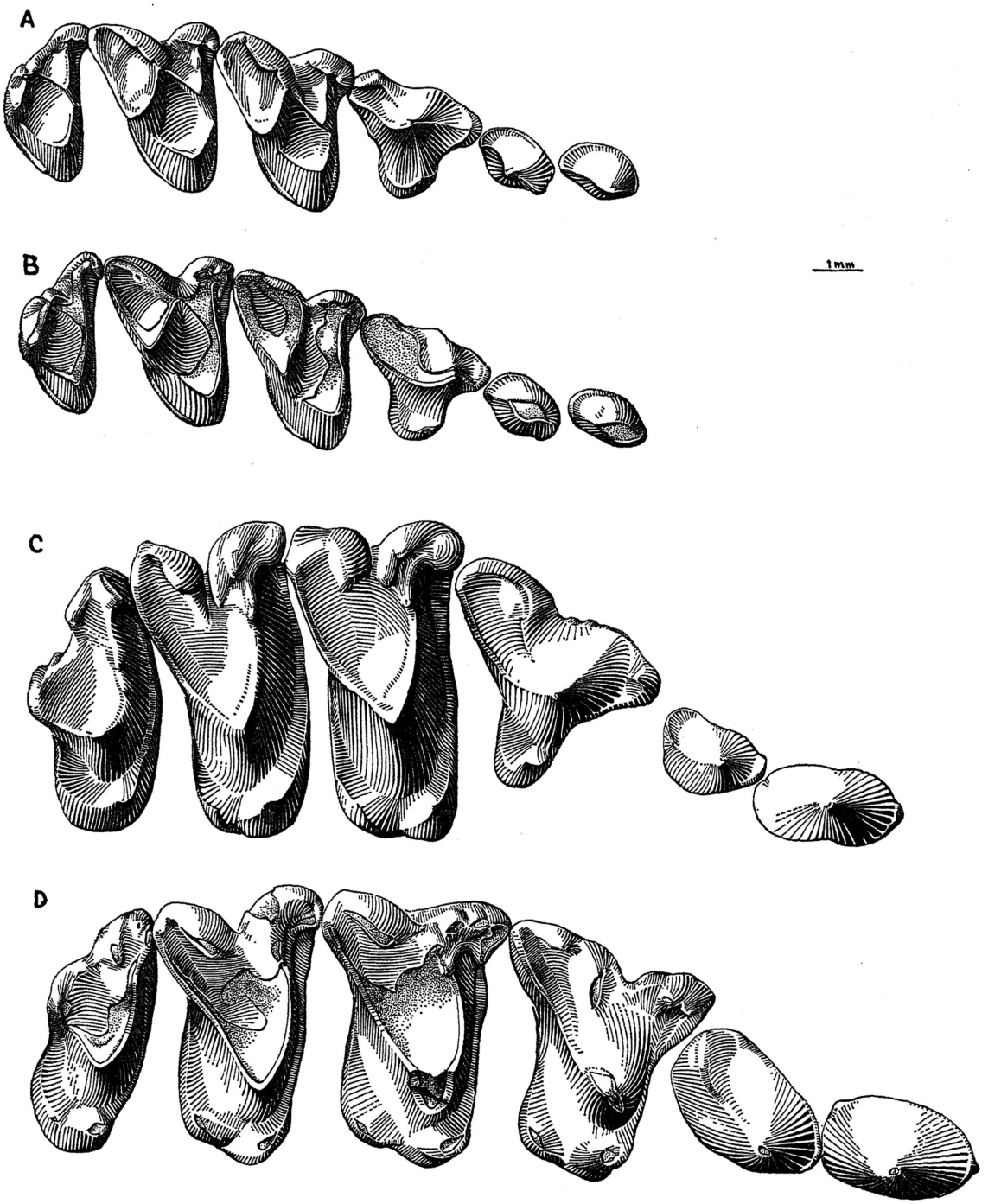

FIG. 11. Occlusal views of upper cheek teeth. A. *Nesophontes edithae*, unworn. B. Same, worn. C. *Solenodon paradoxus*, juvenile with Pd^2 and Pd^4. D. Same, adult with permanent premolars. C is viewed from a slightly more lingual angle than is D, which accounts for the discrepancy in buccolingual diameter of the molars in the two specimens.

Actually, the dentition is not entirely dissimilar in the two genera, and there is one feature (the buccal stylar crest of the upper molars) in which *Solenodon* and *Nesophontes* resemble each other and differ from all other insectivores.

Nothing of the deciduous dentition of *Nesophontes* is known, save a lower jaw of *N. edithae* (A.M.N.H. No. 17115) that shows a permanent canine in place, with its deciduous predecessor. The very scarcity of specimens with milk dentition among the great number of individuals collected would argue that the deciduous dentition was shed early in life in *Nesophontes*, presumably before the animals became active foragers subject to the attack of owls. (All known material of *Nesophontes* appears to represent the remains of owl pellets.)

The permanent dentition of *Nesophontes* shows the following gross formula:

$$I_3^3\ C_1^1\ P_3^3\ M_3^3$$

This differs from the primitive placental formula only in the absence of one upper and one lower premolar.

The gross dental formula of *Solenodon* is identical to that of *Nesophontes*. In marked contrast to Old World zalambdodonts, ani-

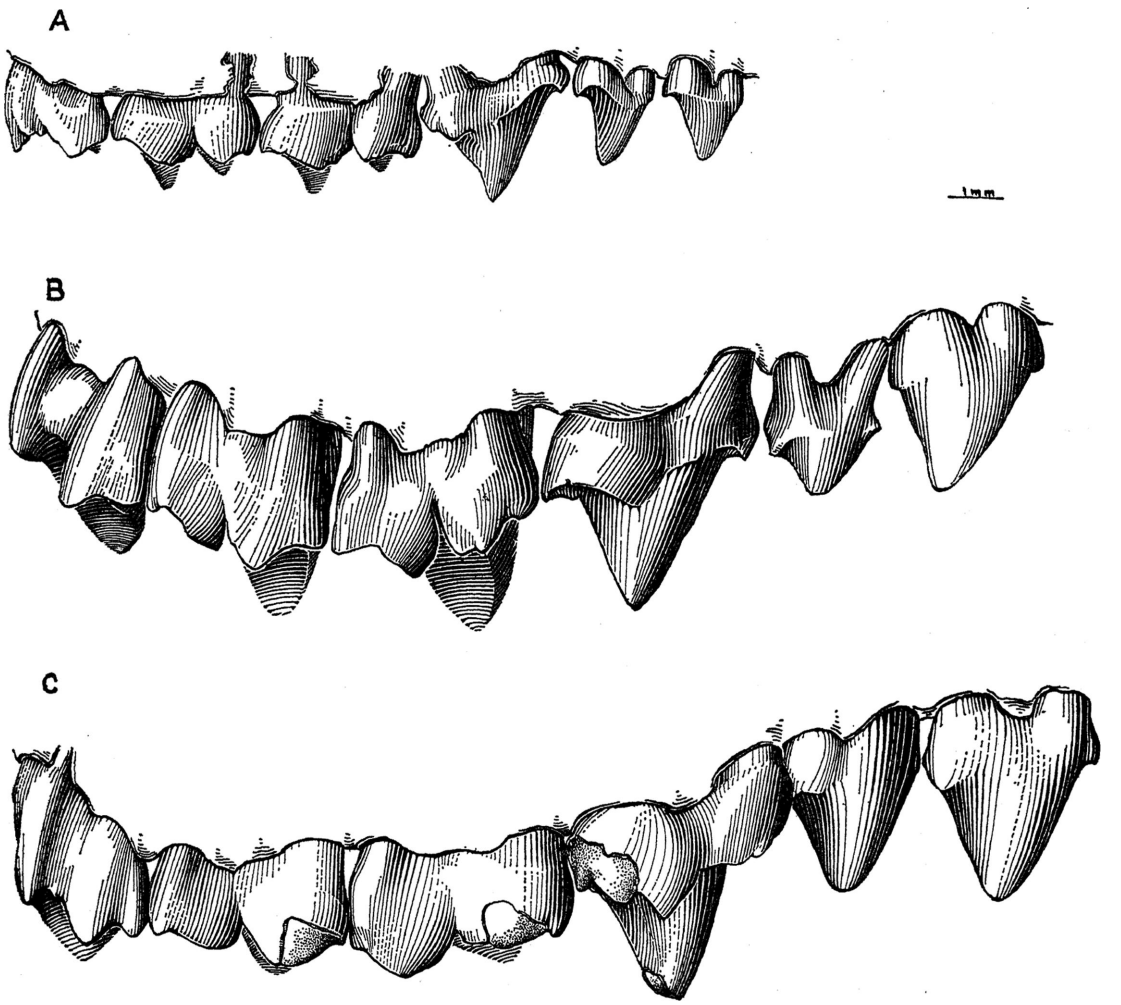

FIG. 12. Buccal view of upper cheek teeth. A. *Nesophontes edithae*. B. *Solenodon paradoxus*, juvenile with Pd^2 and Pd^4. C. Same, adult, with permanent premolars.

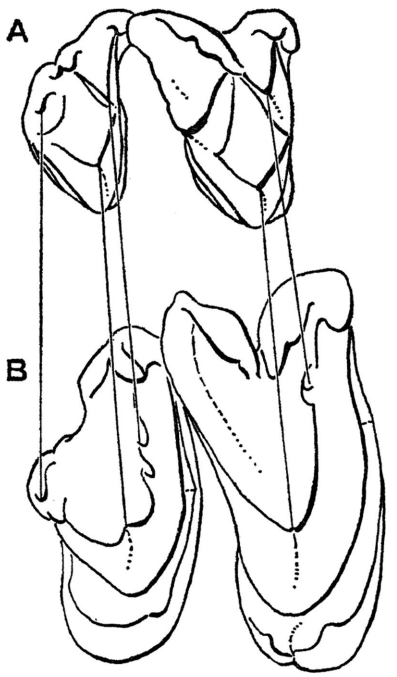

FIG. 13. Last two upper molars. A. *Nesophontes edithae*. B. *Solenodon paradoxus*, showing cusp homologies here suggested.

mals that retain milk teeth until full size is reached, the deciduous dentition of *Solenodon* is shed very early. It should be noted, however, that Pd^4 is replaced after the eruption of all three molars, which is unusual for mammals. The nestlings obtained by human collectors give us a knowledge of the milk teeth of *Solenodon* lacking in the case of owl-collected *Nesophontes*. The two anterior upper incisors, canine, and all but the anteriormost upper premolars have deciduous predecessors in *Solenodon*. It is the rule among placentals for P^1 to be unreplaced, but for P^2 to be locus for both a deciduous and a permanent tooth. Accordingly it seems most reasonable that the foremost upper premolar of *Solenodon* is P^1. The most posterior upper deciduous premolar is of a form usual, indeed characteristic, of the lipotyphlan Pd^4, with a high central cusp and the paracone connected to the metastyle by a long, sloping crest (apparently a rudimentary metacone). Between P^1 and Pd^4 is a single, small, unicuspid tooth placed rather nearer to P^1 than to Pd^4, and conspicuously more like the former than the latter in form. Tentatively and without conviction this tooth may be identified as Pd^2, its successor then being P^2. For want of better evidence, we may assume the lower dentition symmetrical to the upper, giving the following formula for the permanent dentition:

$$I^{1-2-3}_{1-2-3}\ C^{1}_{1}\ P^{1-2-}_{1-2-}\ {}^{-4}_{-4}\ M^{1-2-3}_{1-2-3}$$

There is some reason to suspect that the formula for *Nesophontes* is the same, for the Cuban *Nesophontes micrus* shows precisely the size ratios of upper premolars seen in the deciduous dentition of *Solenodon*, with the most anterior premolar about twice the size of the premolar just behind. Indeed, as may be seen from figures 11 and 12, the upper premolars of *Nesophontes* are very similar in all respects to the upper deciduous premolars of *Solenodon*. The possibility remains, indeed, that in *Nesophontes* the milk premolars persist and their normal successors have been suppressed.

Solenodon differs from the Old World zalambdodonts, as well as from most other mammals, in that the permanent P^4 is more molariform than is its deciduous predecessor.

It is the pattern of sculpture of the molar crown that has caused *Solenodon* to be separated widely from *Nesophontes* in classification. *Nesophontes* shows three main cusps on M^1 and M^2, a rostro-buccal paracone, a caudo-buccal metacone, and a lingual protocone. A narrow cingulum runs along the rostral surface of the tooth, another cingulum along the caudal and lingual surface. The paracone is wedge-shaped, with a rostral commissure that is nearly perpendicular to the midline of the skull, and a diagonally placed caudo-lingual commissure that extends backward and outward from the apex of the cusp. The metacone is approximately double the paracone in all linear dimensions, thus about eight times the volume of that cusp. All its commissures parallel the corresponding commissures of the paracone, to which the metacone is similar in appearance. The protocone is also wedge-shaped, with its anterior commissure essentially a continuation of the paracone, while its posterior commissure continues the curve of the posterior commissure of the metacone.

M^1 and M^2 in *Solenodon* show only one

major cusp located lingually and surrounded by a rather broad cingulum that is divided lingually into two cusps. On the rostral commissure of the main cusp is a small cusp. In general practice (e.g., Butler, 1937) today, the cingulum of *Solenodon* is regarded as protocone and hypocone, the main cusp as paracone, and the small cusp on the rostral commissure of the supposed "paracone" is ignored.

But comparison of M^{1-2} of *Solenodon* with those of *Nesophontes* shows that the position of the "paracone" of *Solenodon* is essentially that of the protocone of *Nesophontes*, while the unnamed cusp on the rostral commissure in *Solenodon* is closely comparable with the paracone of *Nesophontes*. By this interpretation, the molar of *Solenodon* would differ from that of *Nesophontes* chiefly in its broader lingual cingulum and the partial division of the cingulum into two cusps, and in obliteration of the metacone. As the molars of *Solenodon* are higher-crowned than those of *Nesophontes*, and the talonids of the lower molars much reduced, the obscuring of the metacone appears primarily the result of the filling-in of the basin for the hypoconid, so that the occlusal surface of the metacone becomes continuous with the occlusal surface of the protocone.

This interpretation of the molar of *Solenodon* receives support from two sources: (1) the form of M^3 in *Solenodon* and *Nesophontes*, and (2) the occlusion of the teeth in *Solenodon*.

In *Nesophontes* the metacone is greatly reduced on M^3, being represented only by a weak lobe caudal and buccal to the protocone. A similar lobe is present in *Solenodon*, developing its own wear surface later in life. The relations of this lobe in *Solenodon* to the main cusp are precisely those of the metacone to protocone on M^3 in *Nesophontes*. Moreover, in some specimens of *Nesophontes edithae* the rostral and caudal cingula may join lingual to the protocone, which increases the resemblance to the "protocone" and hypocone of *Solenodon*.

When the jaws are articulated and the teeth occluded in *Solenodon*, the main cusp of the upper molars bites well within the buccal margins of the lower tooth row, over the reduced talonids of the lower molars. Thus, when the skull and jaw with occluded molars are viewed from directly beneath, the apex of the main cusp of P^4 (and particularly true of Pd^4) is visible, but the apices of the main cusps of the molars are concealed by the lower jaw and dentition. The exposure of the tip of the main cusp of P^4 is expected, as this is normal for a paracone. The concealment of the main cusps of the molars is to be expected of protocones, not at all normal for paracones.

An alternative explanation is that of G. M. Allen (1918). According to this view the main cusp of *Solenodon* (a cusp we may call noncommittally the "zalambdocone") is homologous to the (hypertrophied and lingually extended) metacone of *Nesophontes*). To my mind this explanation runs into difficulty when we consider serial homologies between M^3 and the other upper molars. The Allen interpretation, however, does have the advantage of precedent, for it fits the facts in evolution of a sort of zalambdodonty in *Coryphodon* from the dilambdodonty of *Pantolambda* (see Simpson, 1929).

The buccal molar styles of *Solenodon* and *Nesophontes* are virtually identical in the two genera and form a structure not seen elsewhere among insectivores, the "notched outer margin" noted by Dobson and quoted by Schlaikjer (1933) in his definition of the Solenodontidae (although it is *not* seen in *Apternodus*, included in that family by Schlaikjer). When the molars are seen in lateral view, they present an outer wall divided into two unequal portions by a deep notch. The smaller anterior portion has a nearly flat outer surface that grades into the outer wall of the parastyle. The larger posterior portion is curled lingually anteriorly onto the occlusal surface. The enamel is chipped, rather than worn down, on this crest, which suggests that it has an axe-like chopping function.

It may be noted that in spite of the undoubted relationship of *Nesophontes* to the Soricidae, the shrews show no suggestion of this crest; instead the fossae bounded by the commissures of the paracone and metacone extend to the extreme buccal margin of the tooth. Similarly, the Old World zalambdodonts, *Apternodus*, and *Palaeoryctes* show no resemblance to *Solenodon* in this regard. The nearest resemblance is seen in some Talpidae, most particularly *Scalopus*, in which the di-

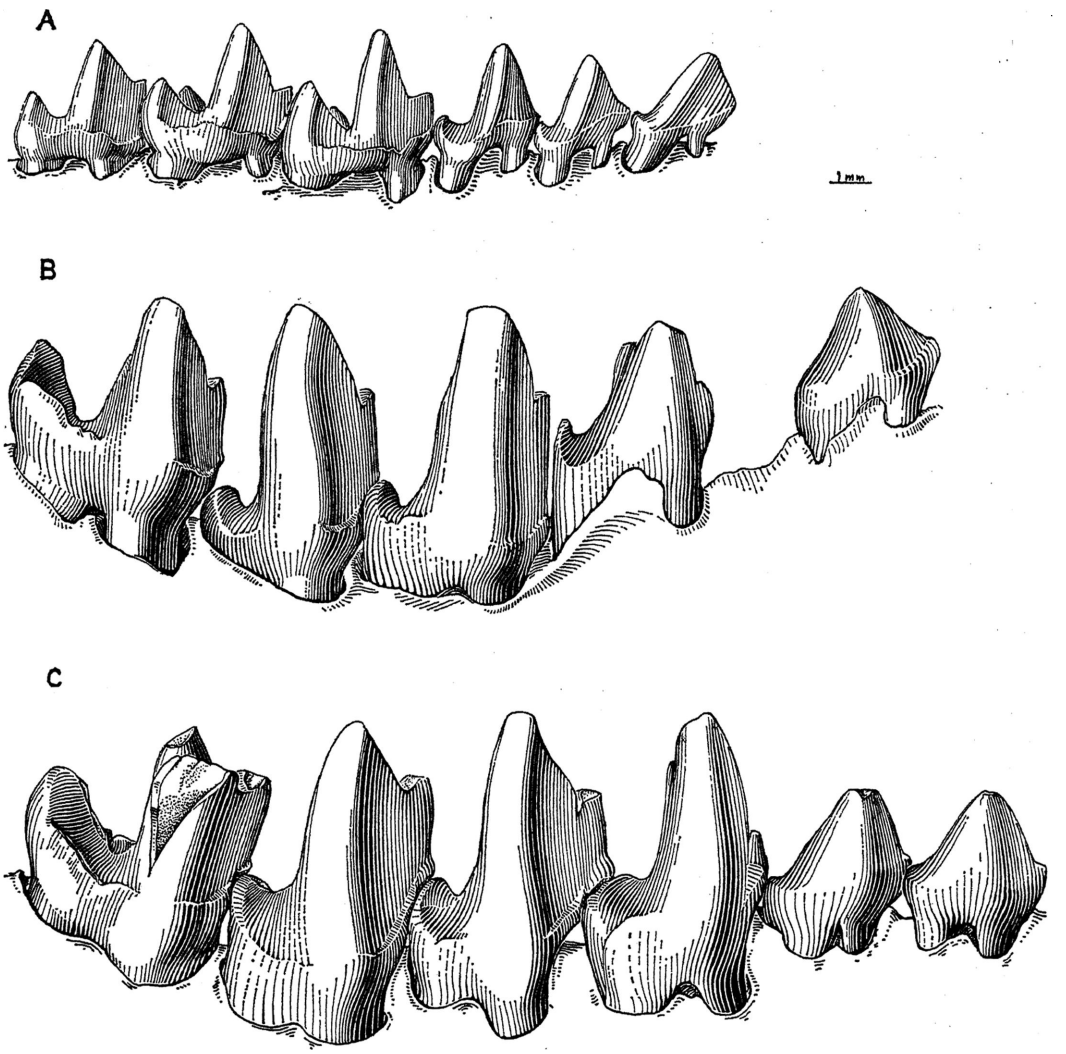

FIG. 14. Buccal view of lower cheek teeth of *Nesophontes* and *Solenodon*. A. *N. edithae*. B. *S. paradoxus*, juvenile with Pd_4 and a gap for the (missing) Pd_2. C. *S. paradoxus*, adult with permanent premolars.

vided mesostyle approximates the notch in the outer molar margin of *Solenodon* and *Nesophontes*, but the webbing from the anterior mesostyle to the parastyle, and from the posterior mesostyle to the metastyle, is not nearly so well developed in moles as in the Antillean genera.

The lower molars of *Solenodon* differ from those of *Nesophontes* in the extreme elevation of the trigonids and reduction of the talonids. In the unworn condition, all the talonid cusps of *Nesophontes* are represented in the tooth of *Solenodon*: a small cusp on the buccal border of the short talonid, adjacent to the base of the protoconid, represents the hypoconid; two cusps that are connate except apically lie at the caudo-lingual corner of the talonid and represent the entoconid and hypoconulid. On M_3 in *Solenodon*, but not in *Nesophontes*, the hypoconulid is greatly enlarged into a hypoconulid lobe that juts upward and backward to occlude with M^3 in a manner closely analogous to a trigonid of a (non-existent) fourth molar.

The main differences between *Solenodon* and *Nesophontes* in molar form appear to be

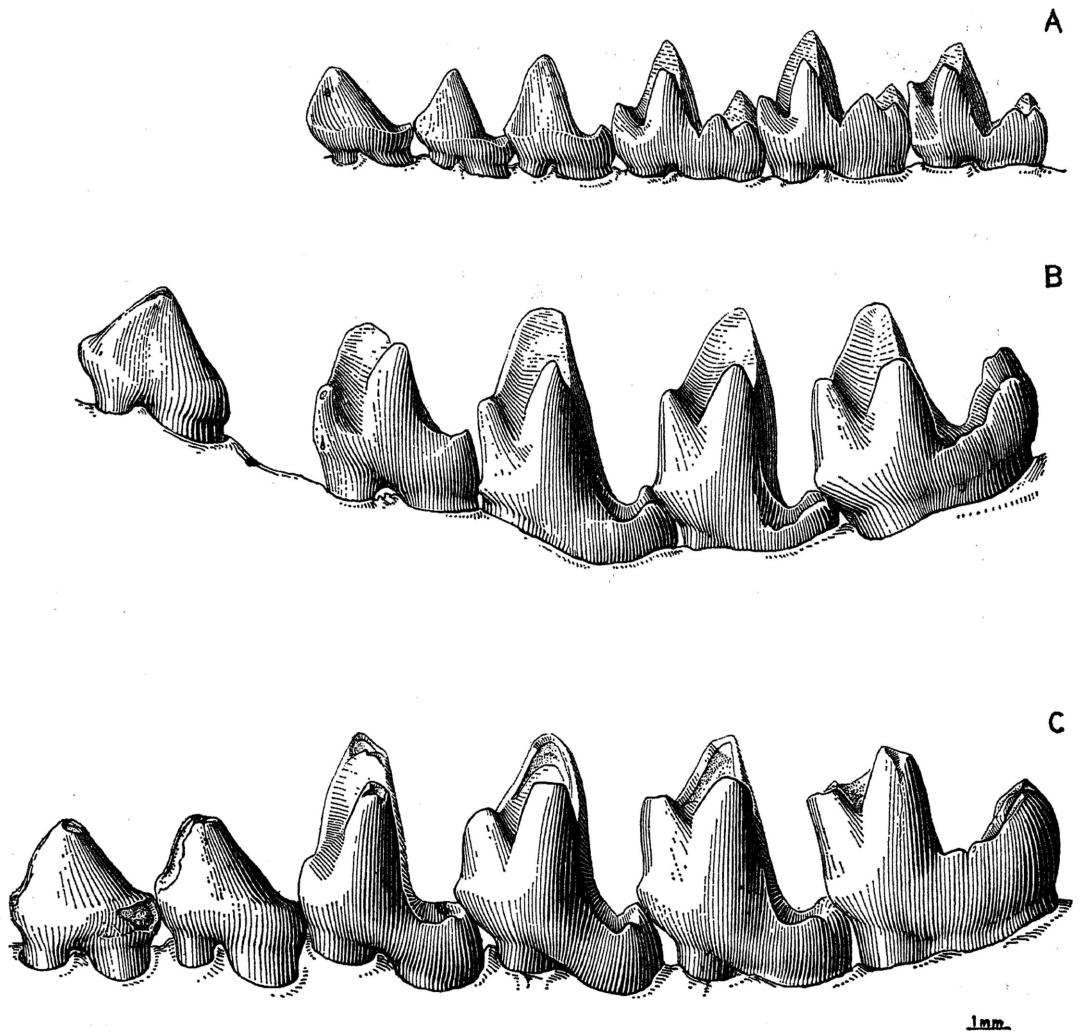

FIG. 15. Lingual view of the lower cheek teeth of *Nesophontes* and *Solenodon*. A. *N. edithae*. B. *S. paradoxus*, juvenile with Pd_4 and a gap for the (missing) Pd_2. C. *S. paradoxus*, adult with permanent premolars.

the result of differences in functional emphasis. In *Nesophontes* the more normal mammalian condition holds, and chewing involves the attrition of the sculpture of the upper molar crowns against the sculpture of the lower molar talonids, most particularly the hypoconids. In *Solenodon*, however, the sculpture of the teeth appears to play little if any part in the function of chewing, and it is the shear of the entire wedge of the upper molar trigon between high lower-molar trigonids that pulverizes the food.

This difference may be functionally related to longevity. Although data on longevity of *Solenodon* and *Nesophontes* are lacking, it is a well-known general rule that larger animals tend to live longer than smaller related species, and it seems reasonable to expect that the large *Solenodon* considerably exceeds the relatively small *Nesophontes* in life span. Now, about one-third of *Nesophontes* molars show an almost excessive wear, so that the paracone is nearly or quite destroyed. Rudd (1955) has shown that in *Sorex vagrans*, an animal related to *Nesophontes* and with essentially similar teeth, the cusps of the molars

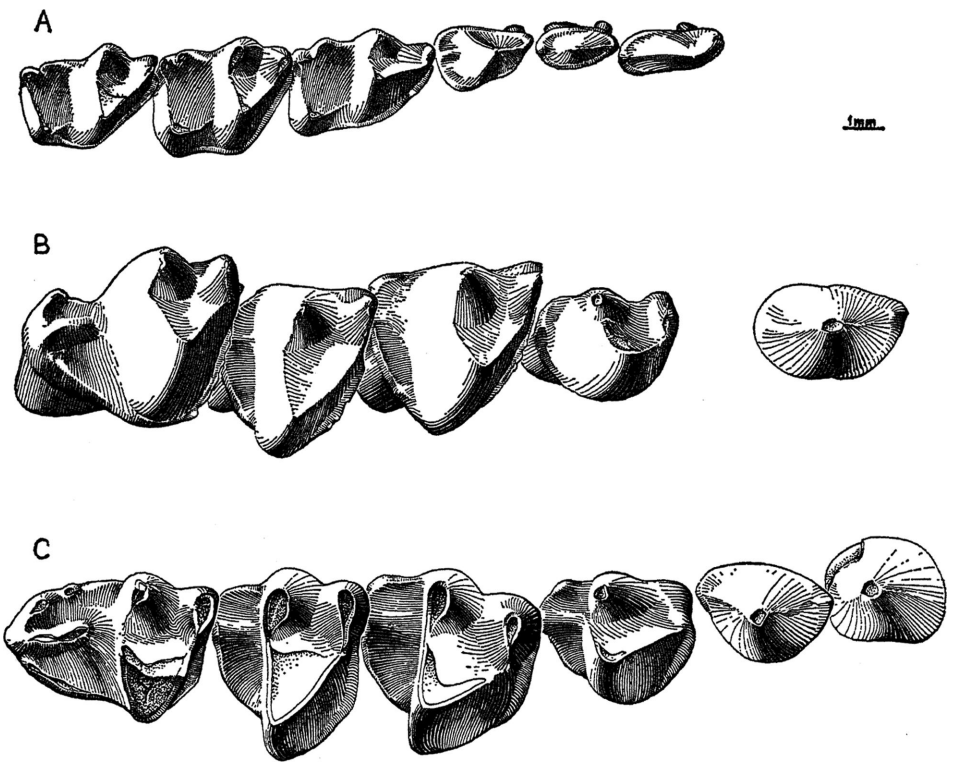

FIG. 16. Occlusal view of the lower cheek teeth of *Nesophontes* and *Solenodon*. A. *N. edithae*. B. *S. paradoxus*, juvenile with Pd_4 and a gap for the (missing) Pd_2. C. *S. paradoxus*, adult with permanent premolars.

are reduced to mere hillocks in individuals 60 to 66 weeks old, and that even these hillocks are gone at 66 to 72 weeks. Obviously, then, the sharp relief of cusps is an efficient triturating surface for only a limited time. Because an aged animal with shrew-like dentition must depend in any case on the gross shear of tooth against tooth, rather than cusp against cusp, it would seem reasonable that natural selection should favor modifications increasing the efficiency of tooth-against-tooth trituration in a form with increased longevity. *Solenodon* would appear to show the culmination of just such a process of natural selection.

There is a great difference between *Nesophontes* and *Solenodon* in anterior dentition, but, oddly enough, the resemblances shown by the respective genera to other insectivores are diametrically opposed to their supposed relationships. Thus, *Nesophontes* is generally believed to be related to the Soricidae, and *Solenodon* to the Tenrecidae; but *Solenodon* is more shrew-like than is *Nesophontes* in anterior dentition, while *Nesophontes* shows several resemblances to the Tenrecidae not seen in *Solenodon*.

In both genera the anteriormost upper incisor is elongated, but the elongation is but moderate in *Nesophontes* and the deciduous dentition of *Solenodon*. The permanent I^1 of *Solenodon* is greatly enlarged, with a large anterolateral lobe and a small subsidiary median lobe. This enlarged I^1 is opposed by an enlarged I_2, while the canines are small. Thus, the anterior dentition of *Solenodon* resolves into an enlarged pair of upper and lower incisors, opposed in forceps-like fashion, separated from the enlarged P^4 and molars by unicuspid teeth. This is decidedly shrew-like, but differs from the soricid condition in the presence of a small incisor anterior to the enlarged lower incisor and in the downward and backward (rather than downward and for-

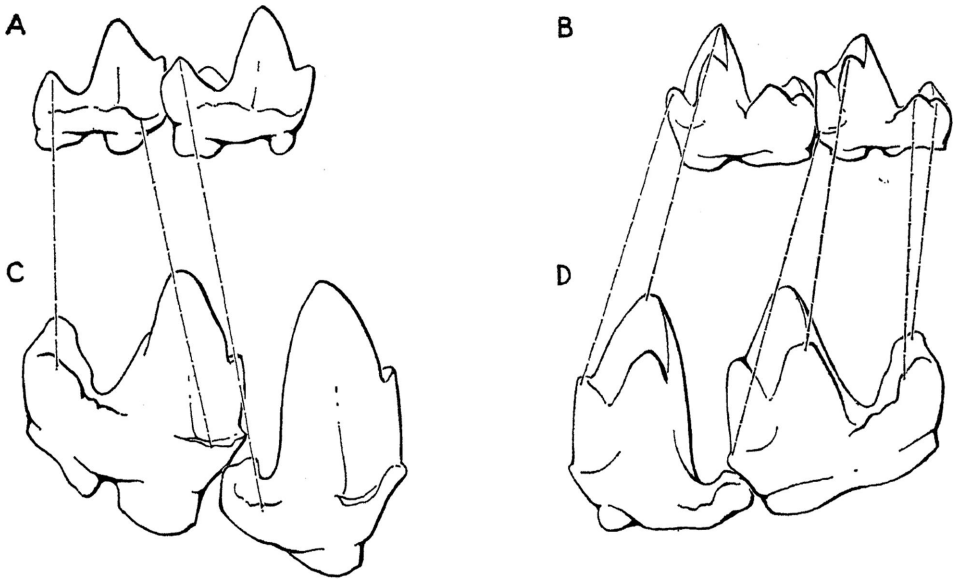

FIG. 17. Homologies here proposed of lower molar cusps in *Nesophontes* and *Solenodon*. The last two molars are shown. A. *N. edithae*, buccal view. B. Same, lingual view. C. *S. paradoxus*, buccal view. D. Same, lingual view.

ward) slant of the enlarged upper incisor. If the Eocene *Saturninia* (Stehlin, 1940) is truly a soricid, and not (as may well be the case) an erinaceid, then the resemblance between *Solenodon* and the Soricidae is increased. *Saturninia* shows a small I_1 anterior to an enlarged I_2. The enlarged I_2 of *Saturninia* shows a crenate margin along the caudo-labial surface of the crown that is strongly suggestive of the sinuated crest on the crown of Id_2 in *Solenodon*. (This crenation of the main lower incisor appears to be the chief reason for referring *Saturninia* to the Soricidae rather than to the Erinaceidae.)

The permanent I_2 of *Solenodon* is remarkably specialized in the presence of a deep and rather broad groove, suggestive of a venom canal (and responsible for the generic name). A suggestion of this groove is presented by at least some soricids (e.g., *Blarina* and *Sorex*), in which a narrow and shallow groove extends along the crown of the enlarged lower incisor, just medial to the crenate ridge.

In *Nesophontes* the lower incisors are subequal and bilobate, with an obtuse sulcus on the lingual surface, while the canines are long and fang-like, giving some resemblance to the tenrecid genus *Oryzorictes*. However, the upper canine of *Nesophontes* is as much *sui generis* as is the second lower incisor of *Solenodon*. The upper canine of *Nesophontes* is trihedral in form, with two canal-like sulci, one extending down the rostral surface, another extending down the lingual surface.

The roots of the teeth are alike in *Nesophontes* and *Solenodon*. The upper canine and first two premolars are two-rooted, the remainder of the upper cheek teeth three-rooted, the upper and lower incisors and lower canine one-rooted (with suggestions of subdivision of the root in I^3 and C_1), and the remaining lower teeth two-rooted.

Both genera show the interradicular crests of Butler on the molars, described for the Erinaceidae by Butler (1948) but characteristic of other Lipotyphla as well. These are raised crests on the faces of the roots facing towards the center of the tooth. On the upper molars the crests meet at a tubercle on the proximal surface of the tooth, equidistant from the roots; the tubercle is pierced by a small vascular foramen. On the lower molars the crests meet to form a prominence in the crotch between rostral and caudal roots. The alveoli show the presence of these crests by presenting corresponding grooves. The buccal roots of each upper molar are nearly circular in section, their regularity interrupted only

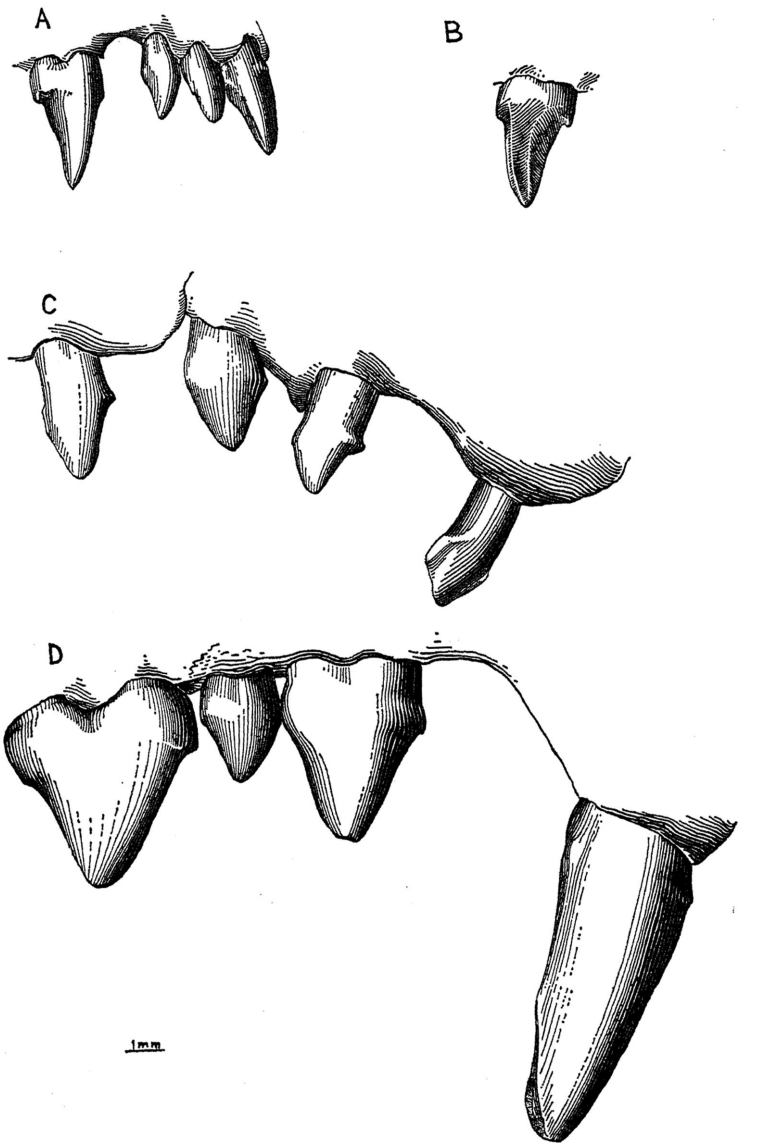

FIG. 18. Upper canine and incisors of *Nesophontes* and *Solenodon*. A. *N. edithae*, labial surface. B. Upper canine of *N. edithae*, lingual surface. C. Juvenile *S. paradoxus* with Id^1, Id^2, and Cd^1, labial surface. D. Adult *S. paradoxus* with permanent incisors and canine, labial view.

by the crests, while the lingual root is slightly oval, with its long axis transverse to the axis of the skull.

NOTES ON THE DECIDUOUS DENTITION OF *Solenodon paradoxus* (A.M.N.H.:M. No. 28272)

J. A. Allen (1908) has given an account of the milk dentition of a nestling *Solenodon paradoxus* (A.M.N.H.:M. No. 28272) obtained by Verrill in 1907. Unfortunately, misprints in the designations of the teeth have garbled Allen's account, so that it is in many ways misleading. For that reason, the present author gives here a redescription of the same specimen.

The specimen apparently was partially disarticulated in 1907 or 1908, for Allen's photo-

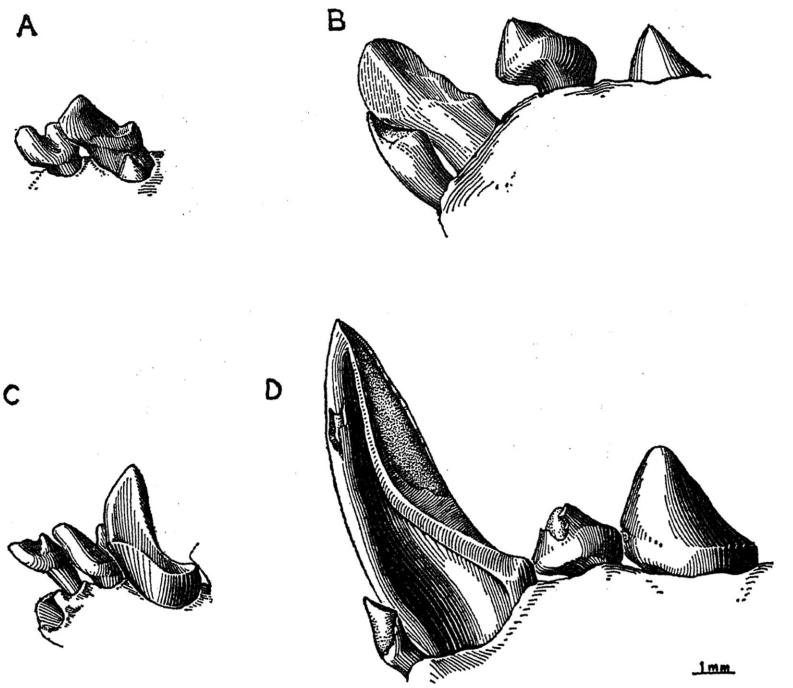

FIG. 19. Lingual view of lower incisors and canine of *Nesophontes* and *Solenodon*. A. *N. edithae*, showing I_3, Cd_1, and the tip of C_1. B. *S. paradoxus* (juvenile), showing I_1, Id_2, I_3, and the tip of C_1. C. *N. edithae*, showing I_2, I_3, C_1, and the alveolus of I_1. D. *S. paradoxus*, showing I_1, I_2, I_3, and C_1.

graphs show the maxilla and premaxilla isolated from the skull. Since that time there has been some loss of parts, one of the palatine bones, for example, being missing from the specimen, still partially disarticulated.

Three incisors are present in the premaxilla, along with their unerupted successors. The first, Id^1, is not enlarged but is very slightly longer than Id^2. Allen's description, "three-sided, with the inner face convex, and the longer diameter transverse to the axis of the premaxillae," is adequate. Allen speaks of "dp^3," apparently a *lapsus* for Id^3, as separated from the canine by the maxillo-premaxillary suture. But the tooth has no replacement and is the definitive I^3. It appears that in *Solenodon*, as in other Lipotyphla, Id^3 is absent. "The canine is similar in form to the adjoining [deciduous] incisor and slightly smaller; consequently many times smaller than the permanent canine." It may be added that the milk canine is single-rooted, as are the milk incisors, rather than double-rooted as is the permanent canine. Allen states that "Dp^1 is similar in form to p^1 and nearly as large," which is not surprising, for it is the identical tooth. No successor is to be seen beneath "dp^1," and P^1 appears to be a monophyodont locus, as usual. Pd^2 is, as stated by Allen, "similar in form to p^1 and nearly as large." The tooth termed dp^3 by Allen is here termed Pd^4, to conform to the practice of using numerical symbols to indicate homology with teeth of the primitive full dentition of 44 teeth, and, similarly, Allen's p^3 is the present author's P^4. Allen's statement that "dp^3" has the same form as "p^3" and is about two-thirds as large is correct as to relative sizes but needs modification as to form. As will be seen from figure 11, the lingual lobe of P^4 is decidedly more molariform than is that of Pd^4.

Allen states that "in the lower jaw id_1 and id_3 have the same form and nearly the same size as i_1 and i_3." It must be pointed out that I_1 and "id_1" appear to be the identical tooth in *Solenodon*, or else Id_1 has already been replaced and lost on both sides in the specimen

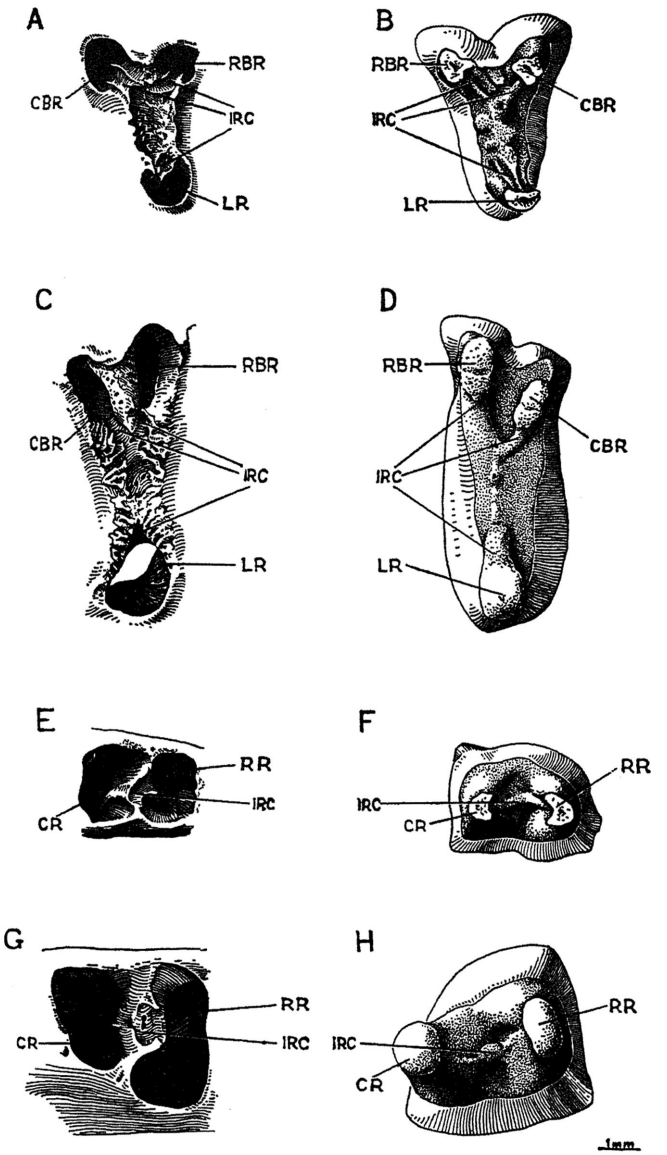

FIG. 20. Dental sockets and alveolar surfaces of molars of *Nesophontes* and *Solenodon*. A. Maxillary socket of M^2 of *N. edithae*. B. M^2 of *N. edithae*. C. Maxillary socket of M^2 of *S. paradoxus*. D. M^2 of *S. paradoxus*. E. Dentary socket of M_2 of *N. edithae*. F. M_2 of *N. edithae*. G. Dentary socket of M_2 of *S. paradoxus*. H. M_2 of *S. paradoxus*. Abbreviations on page 129.

at hand. As the first lower incisor is already rather worn, the second hypothesis seems unlikely. Similarly, Allen's "id^3" appears to be I_3. Allen states "dp_2 [an evident misprint for Id_2] is a small tooth, rather long, laterally flattened and sharp-edged, but wholly lacks the inner groove so conspicuous in i_2, and is only about one tenth as large." This statement is substantially correct, but it should be noted that one-tenth is an optical estimate of the volume ratio and is a gross exaggeration of any difference in linear dimensions between

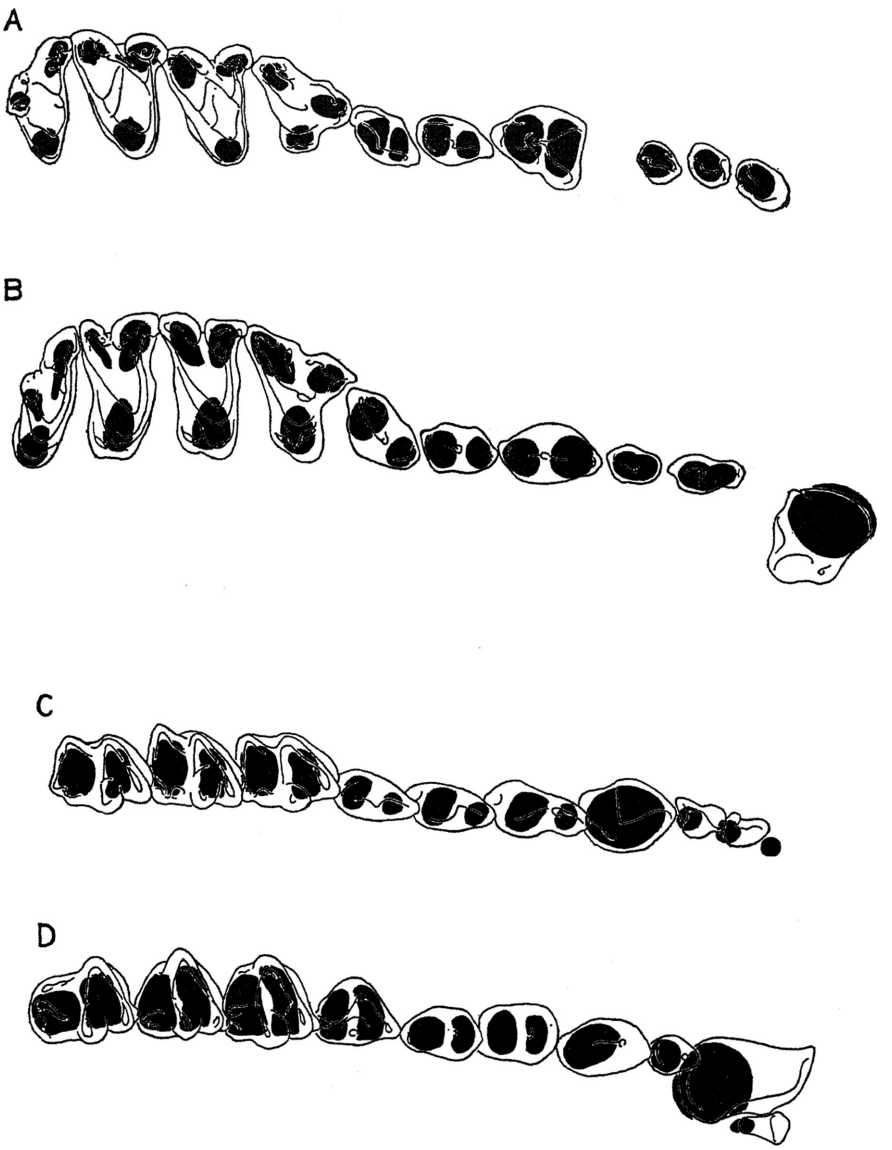

FIG. 21. Pattern of dental roots in *Nesophontes* and *Solenodon* (not to same scale). A. *N. edithae*, upper dentition. B. *S. paradoxus*, upper dentition. C. *N. edithae*, lower dentition. D. *S. paradoxus*, lower dentition.

Id_2 and I_2. Allen does not describe the rather conspicuous festooning of the posterior cutting edge of this tooth.

According to Allen, Cd_1 is very small and but a mere point. This tooth appears to have been lost from the specimen since Allen's description, but it is shown in Allen's photograph. He further notes that "pd_1 is nearly as large as p_1 and of the same form." As in the upper jaw, the first premolar appears to be a monophyodont tooth, without indication of an underlying successor; thus, "pd_1" is really P_1. Allen continues: "dp_1 [an evident misprint for Pd_2] has fallen out and its successor protrudes above the alveolus; it has been preserved and is a minute conical tooth (not shown in the photograph . . .)." Unfortunately, since Allen wrote, this "minute conical tooth" appears to have been lost. It is unfortunate that it was not figured, but Leche

(1907) figures a tooth fitting this description in *Solenodon cubanus*. Allen says, "dp_3 [Pd_4 of the present author's notation] is a relatively large tooth, similar in form to p_3 [my P_4], but about one half smaller." This statement must be qualified by my adding that P_4 is more molariform that Pd_4 in having a higher, more dagger-like protoconid and a relatively more anterior metaconid.

The full dental formula for both permanent and milk teeth in *Solenodon* would appear to be:

$$\frac{I^1\ I^2\ I^3\ C^1\ P^1\ Pd\ —\ P^4}{Id^1\ Id^2\ —\ Cd^1\ —\ Pd^2\ —\ Pd^4\ M^1\ M^2\ M^3}$$

$$\frac{—\ Id_2\ —\ Cd_1\ —\ Pd_2\ —\ Pd_4\ M_1\ M_2\ M_3}{I_1\ I_2\ I_3\ C_1\ P_1\ P_2\ —\ P_4}$$

There is some doubt whether the missing premolars in both upper and lower jaws are the second or the third.

Notes on the Deciduous Dentition of *Nesophontes edithae* (A.M.N.H. No. 17115)

To the present author's knowledge, the only specimen of *Nesophontes* showing milk teeth is a lower jaw (A.M.N.H. No. 17115) of the Puerto Rican *N. edithae*. This specimen shows the milk canine in place, with the tip of the permanent canine just emergent beneath it. The milk canine is much lower than the permanent canine, with its main cusp more forwardly inclined and the posterior cingulum stronger and more decidedly cusp-like. Anthony (1925) has correctly described the milk canine as premolariform, as compared with the permanent canine, but, because of the peculiar form of the incisors in *Nesophontes* (shared with some Tenrecidae), the tooth might also be described as partially incisiform. That is, its main cusp is relatively low, blunt, and forwardly inclined, as is the main incisor cusp, while the posterior cingulum cusp of the milk canine is quite similar to the posterior lobe of the bilobate incisors.

Just anterior to the canine is the bilobate I_3. X-ray exposures show that this tooth has a root extending deeply into the dentary, with no replacement underlying it; thus, it cannot be Id_3.

The alveolus of I_2 is equal in size to that of I_3 and appears to be empty. However, deep inside the alveolus is a small and hollow enamel cap, obviously I_2 in an early stage of development. As the alveolus shows every sign of having been occupied by a tooth at least as large as I_3, this tooth, now lost, must have been Id_2.

The alveolus of I_1 is entirely empty and contains no tooth rudiment. This suggests that I_1 is a monophyodont locus.

The crown and posterior root of P_1 are absent, but the anterior root remains in place, while the two posterior premolars are complete. X rays reveal that no replacement teeth exist in the dentary beneath the exposed teeth. Possibly milk premolars existed at one time but were already replaced before death. However, the very rudimentary state of the permanent I_2 and the retention of Cd_1 suggest that any deciduous premolars that may have existed should still be in place, and a similar argument holds for the incisors. Tentatively, then, we may give the following formula for the dentary teeth:

$$\frac{—\ Id_2\ —\ Cd_1\ —\ —\ —\ —\ M_1\ M_2\ M_3}{I_1\ I_2\ I_3\ C_1\ P_1\ P_2\ —\ P_4}$$

Alternatively, it is possible that in *Nesophontes* the replacement premolars are suppressed and the milk premolars retained throughout life. This is suggested by the similarity of the upper premolars to the milk premolars of *Solenodon*.

That at least two deciduous teeth, Id_2 and Cd_1, were present in *Nesophontes* appears to be firmly established. This increases the distinction between *Nesophontes* and the Soricidae, for the soricids have the milk dentition almost entirely suppressed and totally uncalcified (cf. Årnback-Christie-Linde, 1912; Woodward, 1896). The resemblance of *Solenodon* is similarly increased, but in the probable absence of milk lower premolars *Nesophontes* is advanced beyond *Solenodon* and makes some approach to the shrews.

Nothing is known of the upper deciduous dentition of *Nesophontes*.

Postcranial Osteology

As the fossil forms that have been supposed to have relationship to *Solenodon* are known

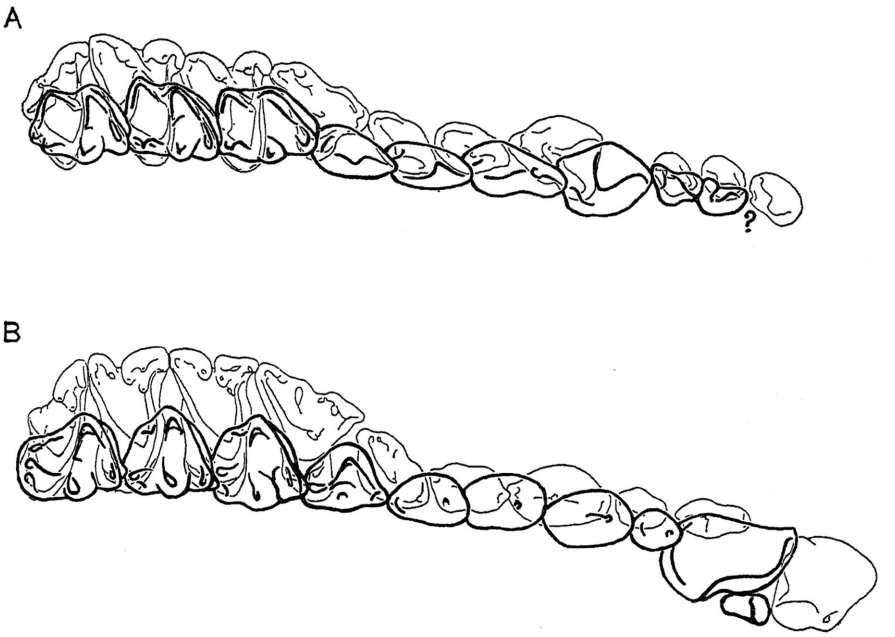

FIG. 22. Occlusion diagrams. A. *Nesophontes edithae*. B. *Solenodon paradoxus*. (Not to same scale.)

only from skulls, resemblances between *Solenodon* and *Nesophontes* cannot be considered critical; hence are only briefly noted here. Anthony (1918, 1925) has figured the postcranial osteology of *Nesophontes edithae* and made comparisons with *Solenodon*. G. M. Allen (1918) has given a brief statement of the results of a comparison of limb bones of *Solenodon* with those of *Nesophontes micrus*.

It is impossible to compare vertebral numbers in the two genera, for all *Nesophontes* finds so far made have been of the jumbled, disarticulated bones remaining after the decomposition of owl pellets, usually representing several individuals hopelessly confused. However, most or all of the vertebrae appear to be represented by at least one specimen.

The atlas appears to differ only in size in the two genera, while the axis differs only in the proportionately smaller size of the neural spine in *Nesophontes*, a difference that might well be accounted for by relative growth factors in animals of such unequal size. The remaining vertebrae are also similar in *Nesophontes* and in *Solenodon*, but differ primarily in development of neural spines. These spines are present but small on the postaxial cervicals of *Solenodon*, altogether absent on corresponding vertebrae of *Nesophontes*; in the lumbar region, the neural spine arises from nearly the entire length of the neural arch in *Solenodon*, only from the anterior portion of the arch in *Nesophontes*.

In the pectoral limb and girdle there is marked resemblance between *Solenodon* and *Nesophontes*. The scapula is nearly identical in the two genera, differing, of course, in size and in that the anterodorsal corner is somewhat more rounded in *Solenodon*. The reduction of the metacromion to a blunt lobe of the spine dorsal to the acromion unites *Solenodon* and *Nesophontes* and sets them apart from most insectivores. The similarity in the form of the humerus of *Nesophontes* to *Solenodon* is striking and probably important, for the humerus is a bone with much "character" in its various processes and foramina and of considerable taxonomic utility (see, for example, Gregory, 1949). Except for size, the humerus of *Nesophontes* differs from that of *Solenodon* only in that the suprotrochlear foramen is constant and large, rather than variable and (when present) small. Anthony has noted the close similarity of the ulna of

Nesophontes to that of *Solenodon*, the two bones showing no conspicuous differences except for size.

The small *Nesophontes micrus* shows no great approach to *Solenodon* in the form of the radius, the bone lacking the flattening and distal expansion seen in the latter (G. M. Allen, 1918, p. 137). However, the larger *N. edithae* shows a decided approach to *Solenodon* in these features and is essentially intermediate. The manus and carpus of *Nesophontes* are unknown.

The ribs of *Nesophontes* share with those of *Solenodon* the very unusual feature of an expanded distal extremity that is obscurely bifid. This is associated in *Solenodon* with a remarkable expansion of the sternal ribs, and it would be interesting to know if such was the case in *Nesophontes*. Unfortunately, the sternal ribs of *Nesophontes* are unknown.

In the pelvic girdle and limb *Nesophontes* and *Solenodon* show fully as close a resemblance as they exhibit in the pectoral girdle and limb. The pelvis appears to differ only in size. (The mistaken idea that *Solenodon* has a true and direct pubic symphysis as in the Menotyphla appears to have arisen from the erroneous association of a pelvis with Brandt's type of *Solenodon paradoxus*. This has been discussed and cleared up by G. M. Allen, 1910, p. 39. All the material of *Solenodon* available to the present author shows a short pubic symphysis involving a median intermediate connective tissue band, as in *Erinaceus* and other Lipotyphla in which any bridge is present at all.) As noted by G. M. Allen (1918) the femur of *Nesophontes* is essentially a miniature of that of *Solenodon*.

Aside from size, the tibia and fibula of *Nesophontes* are very similar in form to those of *Solenodon*. An additional resemblance between the two genera is the variability of distal fusion. In each of the two genera the fibula either may be quite free of the tibia, or else may be fused by approximately its distal fourth with the latter bone. In the latter case, the zone of juncture is clearly indicated by a groove.

The pes and tarsus of *Nesophontes* are unknown. This is particularly vexing, for one of the most characteristic features of *Solenodon* is the unique (?) articulation of the entocuneiform, which extends over the plantar surface of the navicular to meet the astragalus, as well as the calcaneum (G. M. Allen, 1910, p. 42).

General Remarks on the Comparison of *Nesophontes* with *Solenodon*

The over-all conclusions to be drawn from the above comparisons is that, except for the dentition, the known morphology of *Nesophontes* is remarkably similar to that of *Solenodon*. For most of the skeletal elements, *Nesophontes* appears to differ from *Solenodon* mainly or entirely in size. In skull structure *Nesophontes* shows remarkably close conformity with *Solenodon*, most strikingly in these particulars:

1. Presence in both genera of features of the Lipotyphla in general. Examples are: pattern of carotid circulation through the ear; structure of the alisphenoid canal; position of postglenoid foramen relative to postglenoid process, chorda tympani, and zygomatic root; absence of entotympanic; form of posterior border of false palate; backward displacement of the anterior orifice of the infraorbital canal from its primitive position above P_3; absence of lacrimal tubercle; presence of sinus canal; temporalis insertion extended far forward over orbit.

2. Presence in both genera of features found elsewhere in the Lipotyphla only in the Soricidae, Tenrecidae, and (at least by one interpretation) Chrysochloridae. Examples are: absence of jugal, the zygomatic arch being broadly interrupted; absence of ectopterygoid laminae; strong development of "postglenoid" process.

3. Presence in both genera of features seen elsewhere among the Lipotyphla only in the Soricidae. Examples are: vestigial condition of tympanic wing of basisphenoid; large pyriform fenestra with great reduction of tympanic wing of alisphenoid; ramus inferior of stapedial artery passing through a relatively shallow groove in the preotic crest of the alisphenoid, rather than a deeply incised notch or completely encircled foramen; greatly reduced epitympanic recess; division of glenoid capitular surfaces on squamosal.

4. Presence in both genera of features seen nowhere else among the Lipotyphla. Examples are: position of origin of levator labii superioris proprius; large and funnel-like lacrimal foramen on the orbital margin.

It would appear that a most remarkable coincidence has occurred, if *Nesophontes* and *Solenodon* are not most closely related to each

other. It would be required that the West Indies are occupied by a shrew that has become the most tenrec-like of all shrews, and a tenrec that is the most shrew-like of tenrecs. It would further be required that a most remarkable convergence has occurred between the two genera, not only in the skull characters mentioned above but in at least one dental character (modification of the buccal styles of the upper molars to form the "notched outer border"), in the form of the humerus, femur, scapula, and the distal extremities of the ribs.

The necessity for this great and inexplicable convergence disappears if we but assume that *Nesophontes* and *Solenodon* are phyletically closely related forms that have diverged considerably in dentition. As pointed out in the section on dental comparisons, it is quite possible to interpret the *Solenodon* molar as a derivative of a *Nesophontes*-like molar, and a functional reason for the differences is suggested by probable difference in longevity between the two genera suggested by the pronounced difference in size.

It must be remembered that on oceanic islands, differences between closely related forms appear most strikingly in feeding mechanisms, as attested by several groups of birds. Thus, the Hawaiian Drepaniidae (see Amadon, 1950) show a range in bill formation far greater than seen within any related continental family. The correspondingly varied bill form of the Geospizinae of the Galapagos Islands has been dealt with by Lack (1947). Amadon (1950) has presented figures showing the great differences in bill shape among the Vangidae on Madagascar and among the Callaeidae on New Zealand. The explanation for this is, presumably, that in rapidly proliferating evolution there is strong selection for differentiation of one stock in feeding habits to reduce competition. The limited faunas of oceanic islands allow a single invading stock to occupy diverse feeding niches that would, on the continents, ordinarily be occupied by various groups of more distant relationship to one another.

The considerable difference between *Solenodon* and *Nesophontes* in the structures immediately involved in feeding, coupled with great similarity in cranial and postcranial osteology, is precisely what might be expected of forms that have originated from an adaptive radiation on an oceanic archipelago.

As is argued more fully in a following section, the supposition of close relationship between *Nesophontes* and *Solenodon*, besides explaining the close osteological resemblances between the two genera, also explains many resemblances of *Solenodon* to the Soricidae.

The main objection to considering *Solenodon* as a West Indian derivative of a dilambdodont type closely approximating *Nesophontes* is the existence of certain continental forms thought to show close relationship to *Solenodon*. Comparisons of these forms with *Solenodon* are now in order.

APTERNODUS COMPARED WITH *SOLENODON*

THE BEST KNOWN of the supposed fossil relatives of *Solenodon* is the North American (Chadron, Brulé, and Whitney) genus *Apternodus*, known from two nearly complete skulls (one in the American Museum of Natural History, A.M.N.H. No. 22466, the other in the Museum of Comparative Zoölogy at Harvard College, M.C.Z. No. 17685), as well as several more fragmentary specimens. Independently, two authors have suggested that *Apternodus* is closely related to *Solenodon:* Winge (1941, a translation of a 1917 work), working with published descriptions and figures of *Apternodus*, primarily of the American Museum specimen as described by Matthew in 1910; and Schlaikjer (1933), working with the Harvard specimen. Although Winge has clear chronological priority in this suggestion, it appears to be Schlaikjer's paper that influenced subsequent work.

Recently (1956) Hough has come to the conclusion that the relationship between *Apternodus* and *Solenodon* is at best not proved, and appears unlikely on cranial evidence.

Both the argument of Winge and that of Schlaikjer are closely similar: First the comparisons are limited to the "zalambdodont" Insectivora on the basis of the dentition. Within the Zalambdodonta (Centetidae of Winge's classification), *Apternodus* is more like *Solenodon* than like Tenrecidae in the absence of a tympanic wing of the basisphenoid; hence *Apternodus* is more closely related to *Solenodon*. We may take up the points of this argument in order, first discussing the dental similarities between *Solenodon* and *Apternodus*, then the cranial anatomy.

DENTITION OF *Apternodus*

So far as can be determined, the number of teeth in *Apternodus* is essentially similar to that in *Solenodon*, save that there is one less upper incisor. This difference, as noted by Schlaikjer (1933), is not absolutely certain, as the premaxillary is damaged in all available material. The precise homologies of the upper incisors and of the premolars are unknown, in the absence of any knowledge of milk dentition in *Apternodus*. We may give the following gross dental formula for *Apternodus*, based on the data in Schlaikjer (1934):

$$I_3^2\ C_1^1\ P_3^3\ M_3^3$$

The anterior dentition shows no special resemblance to that of *Solenodon*. As noted above, probably only two upper incisors are present in *Apternodus*. The alternative interpretation is that an additional upper incisor was present anterior to the two preserved incisors, but its alveolus has been broken off.

The proportions of the lower incisors in *Apternodus* differ not only from those of *Solenodon*, but from the proportions seen in all Lipotyphla. In the Lipotyphla I_2 is equal to I_3 (e.g., *Nesophontes*), or I_2 is enlarged (e.g., *Solenodon*), whereas in *Apternodus* I_2 is reduced to a minute vestige, while I_1 is enlarged. In the Lipotyphla I_1 is usually either small (e.g., *Solenodon*, *Nesophontes*) or absent (e.g., *Erinaceus*), but is enlarged in some Echinosoricini (e.g., *Hylomys*).

The upper canine of *Apternodus* is similar to that of *Solenodon*, neither genus showing the peculiar development seen in *Nesophontes*. It is two-rooted and obtusely conical in both genera. The lower canine of *Apternodus* is one-rooted and obtusely conical, again being more like the lower canine of *Solenodon* than is that of *Nesophontes*. (It is not certain that "C^1" of *Apternodus* is not really P^1, but its replacement in *Solenodon* shows definitely that the tooth in the Antillean genus is the canine.)

The roots of the cheek teeth of *Apternodus* show no indications of the interradicular crests of Butler seen in *Solenodon*, *Nesophontes*, and the other Lipotyphla (particularly the Erinaceidae; see Butler, 1948). Moreover, the buccal roots of the upper molars appear to be relatively much larger than in the Lipotyphla. (This is based on the Harvard specimen, in which breakage has revealed the roots of one of the upper molars. The type material of *Apternodus midaevus* reveals the absence of grooving between alveoli of the lower cheek teeth, showing that interradicular crests are absent.) The number of roots in *Apternodus* appears to be the same as in *Solenodon* and *Nesophontes*, except that

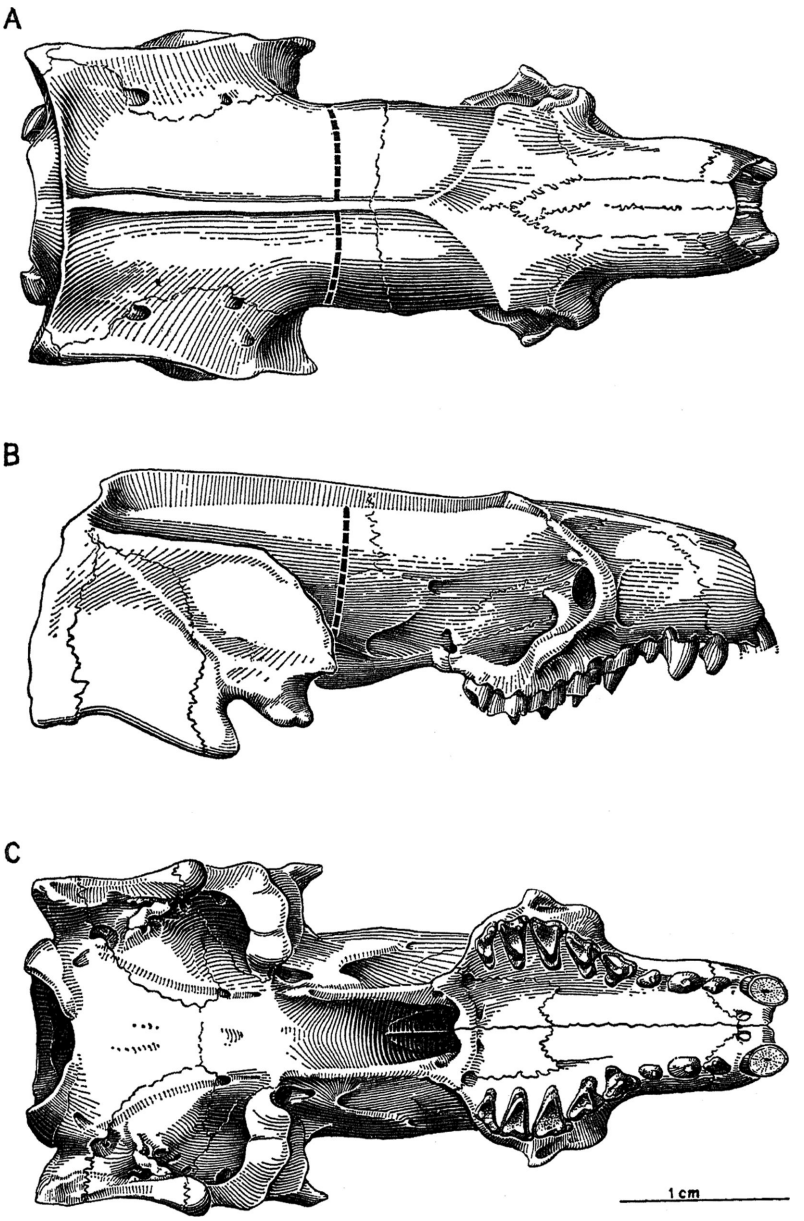

FIG. 23. Skull of *Apternodus*, based primarily on the type of *A. brevirostris* (A.M.N.H. No. 22466), but with missing parts drawn in from the type of *A. gregoryi* (M.C.Z. No. 17685). Dotted line indicates the probable line of contact of the cribriform plate with the skull wall, as determined on M.C.Z. No. 17685. A. Dorsal view. B. Lateral view. C. Ventral view.

the anteriormost lower premolar is single-rooted rather than two-rooted.

In spite of the fact that it is the "zalambdodont" molar form of *Apternodus* that has led most workers to the association of the genus with *Solenodon*, the resemblance between the two genera in molar form is anything but detailed. Indeed, even Schlaikjer (1933) admitted that among living "zalambdodonts" it is *Microgale*, rather than *Solenodon*, that

most closely resembles *Apternodus* in molar form.

The buccal styles of the upper molars of *Apternodus* show no indication of the notched secant crest formed in both *Solenodon* and *Nesophontes*. The small cusp on the anterior border of the molar crown in *Solenodon*, here identified as the paracone, is totally absent in *Apternodus*, while the rather poorly marked metacone on M^3 of *Solenodon* is not suggested in *Apternodus*. The characteristic hypocone of *Solenodon* is absent in *Apternodus*.

The occlusion of the cheek teeth in *Apternodus* does not confirm homology of the main upper molar cusp with that of *Solenodon*. For convenience, the main upper molar cusp of the various "zalambdodonts" is here termed the zalambdocone. As argued in the previous section, the occlusion of the zalambdocone in *Solenodon* suggests that it is the protocone, as it bites far linguad and is unlike the paracone of the premolars in that it is concealed from direct ventral view by the lower dentition when the jaws are articulated. In *Apternodus*, however, the zalambdocones of the upper molars are revealed to direct ventral view when the lower dentition is occluded and resemble in position the paracones of the premolars. Such a position of the zalambdocone is most nearly approximated among living mammals by the Australian marsupial *Notoryctes*, although it is clear that *Apternodus* is a placental and that the resemblance is fortuitous.

The upper premolars of *Apternodus* differ from those of *Solenodon* in showing a graded and even approximation to a molar-like form, from the anteriormost simple and conical tooth to the last, completely molar-like tooth. The transition is much more abrupt in *Solenodon*, the anterior two premolars being simple, the third abruptly submolariform. It is noteworthy that the abrupt change in size and form from middle to last upper premolar is a characteristic that *Solenodon* shares with *Nesophontes*.

In the lower premolars, *Apternodus* differs from *Solenodon* in a manner parallel to the differences shown in the upper premolars; that is, the middle one of the three premolars is intermediate in size and complexity between the anterior and the posterior premolars, whereas in *Solenodon* the first two premolars are very similar to each other and markedly smaller and more simple than the last premolar. *Solenodon* and *Apternodus* resemble each other and differ from *Nesophontes* in that P_4 is complicated and submolariform; however, the method of complication does not appear to be the same in *Apternodus* and *Solenodon*. In *Apternodus* the trigonid of P_4 is fully molariform, with strong paraconid, but in *Solenodon* the trigonid of P_4 appears to represent only the protoconid of the molars, with a strong suggestion of the metaconid, but no indication of the paraconid. On the other hand, the talonid is unrepresented on P_4 in *Apternodus*, whereas in *Solenodon* there is a talonid on the last premolar fully as large as that on the first two lower molars.

The full significance of dental resemblances and differences between *Solenodon* and *Apternodus* is discussed more fully in a later section, but it appears clear that the only special dental resemblance between *Apternodus* and *Solenodon* is zalambdodonty, and that even here there is no detailed resemblance. The occlusion pattern of the molars suggests that in *Solenodon* the zalambdocone represents the protocone, whereas the zalambdocone of *Apternodus* is serially homologous with the paracones (or, for those who prefer the term, amphicones) of the premolars.

The Skull of *Apternodus*

The general form of the skull in *Apternodus* does not greatly resemble that of *Solenodon*. Most conspicuous of the differences is the formation of lateral auditory plates in *Apternodus*. The nature of these plates was made clear by Schlaikjer (1934). The main portion of the auditory plate is formed by the mastoid, which is exposed laterally but totally lacks posterior exposure. The posterior portion of the auditory plate is formed by the hypertrophied paroccipital process, which is closely joined with the mastoid process. The squamosal forms the anterior portion of the plate, with the result that the glenoid fossa and postglenoid process are mounted at the anteroventral corner of the auditory plate. The lateral surface of the auditory plate is flattened and actually slightly concave. A sharp ridge of bone, defining the auditory plate from the fossa for the temporal muscle, runs along the anterior and dorsal border of the plate, from the glenoid fossa to the occi-

put, where this crest joins the nuchal crest at a slightly acute angle. Posteriorly, this auditory plate appears to be solidly formed by the mastoid and exoccipital bones, although this has not been demonstrated by dissection. Anteriorly, however, this plate is hollowed out internally by a deep and large fossa in the roof of the tympanic cavity, this fossa apparantly lying in the squamosal and set off from the remainder of the middle ear by a diagonal crest of bone. Thus it appears that the anterior portion of the auditory plate lodges an exceptionally large epitympanic recess and is thus suggestive of the inflated temporal bulla of *Chrysochloris*, although so different in detail that no special resemblance to that genus is indicated. The auditory plates give the skull great width and render the occiput much broader than deep and transversely concave.

It must be noted that of all the Lipotyphla, *Solenodon* shows the least approach to the unique temporo-occipital region of *Apternodus*. Thus, *Solenodon* has relatively the narrowest and most compressed temporal region of living insectivores and, rather than showing the hypertrophy of the paroccipital process seen in *Apternodus*, differs from other Lipotyphla in the feeble development of this process. The occiput of *Solenodon* is much more deep than broad and is transversely convex; it is, indeed, more extended posterior to the level of the paroccipital processes than is usual in insectivores. Rather than having a large epitympanic recess, *Solenodon* agrees with the Soricidae and *Nesophontes* in having a much reduced epitympanic recess.

In *Apternodus* the snout, as measured from the anterior border of the orbit, is very short, about one-fourth of the total length of the skull; the proportions might be said to be "mustelid." In *Solenodon* the snout is elongated and the proportions are more "canid," the snout being equal to nearly half of the condylobasal length of the skull. Moreover, while the snout of *Solenodon* is compressed, with flattened sides, the snout of *Apternodus* is essentially cylindrical, so that the premolar tooth rows are more medially set than the lateral borders of the rostrum.

Whereas the nuchal crest of *Solenodon* is strongly developed and directed backward, strongly overhanging the occiput, in *Apternodus* the nuchal crest is much weaker, vertical, and, rather than overhanging the occiput, is anteriorly displaced so that the occiput is narrowly visible from above.

The jugal arch is absent in *Apternodus*, as in *Solenodon* and *Nesophontes*, but the resemblance is not detailed, for there is no trace of the pointed maxillary and squamosal roots in *Apternodus*, while these are strongly developed in the two West Indian genera.

In both *Solenodon* and *Nesophontes* the sagittal crest is low and forked anteriorly into a pair of curved, faint ridges that extend to the region of the lacrimal foramen, the temporal muscle extending to the level of the front of the orbit. But in *Apternodus* the sagittal crest is much higher and anteriorly divides into a pair of strong, diagonal crests that extend to a pair of short, obtuse, postorbital processes *behind* the orbit, which indicates that the temporal muscles do not extend over the orbit.

In short, there is but little, if any, special resemblance between *Solenodon* and *Apternodus* in the general form of the skull, nor has any been claimed. Matthew (1910) considered that, in so far as *Apternodus* resembles any living "zalambdodont" in general form of the skull, the resemblance is to the tenrecid *Setifer*. Both Winge (1941) and Schlaikjer (1933) recognize the great specialization and peculiarity of the skull of *Apternodus*. Their argument is based on a detail of basicranial structure, the absence of a tympanic wing of the basisphenoid. The great reduction of this structure in *Solenodon* is, indeed, a most important feature and sets the genus apart from all other Lipotyphla save *Nesophontes* and the Soricidae. However, before much weight can be attributed to this feature in *Apternodus* it must first be established that the latter genus is a lipotyphlan, for the absence of a unique lipotyphlan feature in a form that is not a member of that group is scarcely remarkable. As shown by the following comparisons, *Apternodus* does not show any of the distinctive features of the Lipotyphla and thus would appear to be not only unrelated to *Solenodon*, but remote from the hedgehogs, shrews, moles, and Afro-Malagasy tenrecs. [Hough (1956) claims that the basisphenoid tympanic wing is present in *Oligoryctes*, a genus probably closely related to *Apternodus*. However, this is not clear from the specimen and appears rather to be but a

slight selvage of the basisphenoid against the ear chamber and does not have the characteristic position of the lipotyphlan basisphenoid wing, abutting against the Eustachian cartilage.]

As Butler (1956) has indicated, the course of the internal carotid artery through the tympanic cavity is quite characteristic of the Lipotyphla. As this pattern is illustrated and described for *Solenodon* and *Nesophontes* in the section comparing those genera (see above p. 139), repetition is unnecessary here. In the present writer's experience the departures from this pattern among the Lipotyphla are even less than stated by Butler. Thus, while the ramus inferior of the stapedial artery in some talpids may appear to pierce the roof of the tympanic cavity, when viewed within the middle ear, actually the artery does not pierce the petrosal or enter the cranial cavity; rather it enters a separate ossified sheath and follows the same course as the ramus inferior of other Lipotyphla. Similarly, in *Tenrec* the ramus inferior follows the normal lipotyphlan course and does not pierce the roof of the tympanic chamber; a small foramen for its exit exists in the preotic crest, near the squamosal-alisphenoid suture, in the same position as the considerably larger foramen for the artery in *Setifer* and *Echinops*. Indeed, although at one time the present author searched diligently for differences between families in tympanic arterial pattern, he has been unable to discover any notable departures from this pattern among the Lipotyphla.

Apternodus, however, shows a very different arterial pattern from that of the Lipotyphla, being perhaps more like that of creodonts in this regard. The carotid artery does not appear to cross the promontorium, for the latter is quite smooth, without indication of a groove for an arteria promontorii but grooved for a stapedial artery. Instead, a groove, undoubtedly for the internal carotid, runs along the most medial portion of the petrosal, medial to the promontorium, to a foramen between the sphenoid and petromastoid mesial to the ear. Posteriorly this groove lies on the basioccipital. Anteriorly, on the border of the ear region, lies the posterior orifice of the pterygoid canal, while a short narrow groove leads from this foramen to the roof of the tympanic chamber. There is a faint continuity from this groove, presumably for a small artery of the pterygoid canal, to the main carotid groove in the American Museum specimen. The course of the carotid in the ear region is thus of the creodont type rather than primate-insectivore type, and essentially similar to that of the oxyaenid *Patriofelis* as figured by Denison (1938). The stapedial artery runs to a discrete foramen in the petromastoid, rather than to the pyriform fenestra as in *Solenodon* and *Nesophontes*.

There is no possibility in the case of *Apternodus* of confusion between the groove for the internal carotid artery and the passage for the inferior petrosal sinus (vein). In this genus a flange of the petromastoid underlaps the edge of the basioccipital, thus enclosing the inferior petrosal sinus within the skull except at the relatively small and round foramen lacerum posterius. This flange of the petromastoid forms a bony wall separating the carotid artery (morphologically ventral). This restriction of the external exposure of the inferior petrosal sinus is in itself a departure from conditions in most Lipotyphla (including *Solenodon*), for in the majority of Lipotyphla the sinus is exposed ventrally by a slit-like forward extension of the posterior lacerate foramen extending nearly or quite to the basioccipital-basisphenoid suture. In the Talpidae (and, to a lesser degree, the Erinaceidae) the exposure is limited to a sharply defined, posterior, lacerate foramen, but this is by the lateral extent of a flange of the basioccipital, rather than by any flange of the petromastoid.

The promontorium of *Solenodon* and *Nesophontes* bears, behind the fenestra rotunda, a tab-like process that supports the tympanic. The process is present in the other Lipotyphla, being weak in young *Tenrec* and in *Erinaceus*, but even better developed in *Potamogale* and *Micropotamogale* than in *Solenodon*. But in *Apternodus* there is, instead, a laterally directed spine behind the fenestra rotunda that meets the mastoid just behind the posttympanic process of the squamosal. Thus, the petromastoid forms a complete bony ring around the stylomastoid foramen. A complete ring is also formed in the Tenrecidae, but here it is by a process (?tympanohyal)

that juts mesiad to meet the promontorium from an origin lateral to the facial nerve.

In the Lipotyphla the postglenoid process is either absent (Erinaceidae, Talpidae), or peculiar in its relationships in that it is grooved posteriorly and more laterally than medially for the chorda tympani, and thus, by inference, lies dorsomedial, rather than lateral, to Meckel's cartilage. This process tapers to a rounded point that opposes the posteromedial extremity of the dentary condyle. Moreover, this "postglenoid" process is continuous with the crest of the alisphenoid (preotic crest) leading to the pterygoid lamina. The most reasonable explanation of this is to follow Gregory (1910) in regarding the "postglenoid process" of those Lipotyphla in which it is present as an entoglenoid process that has become modified to fulfill the function of bracing the jaw articulation, in addition to its primitive function of bounding the middle ear. The absence of the true postglenoid process in shrews, tenrecids, *Solenodon*, and *Nesophontes* might well be explained by their ultimate origin from the Erinaceidae, in which the process is absent.

In *Apternodus*, however, the postglenoid process is probably homologous with that of the majority of mammals, for it is sharply set off from the pterygoid crest, is the most laterally produced portion of the skull, and abuts against the entire posterior surface of the condyle. It is grooved for the chorda tympani medial to its midpoint. The postglenoid (venous) foramen is anomalous in being in the epitympanic recess, a probable consequence of the large size of the recess and the presence of temporal plates. But the postglenoid

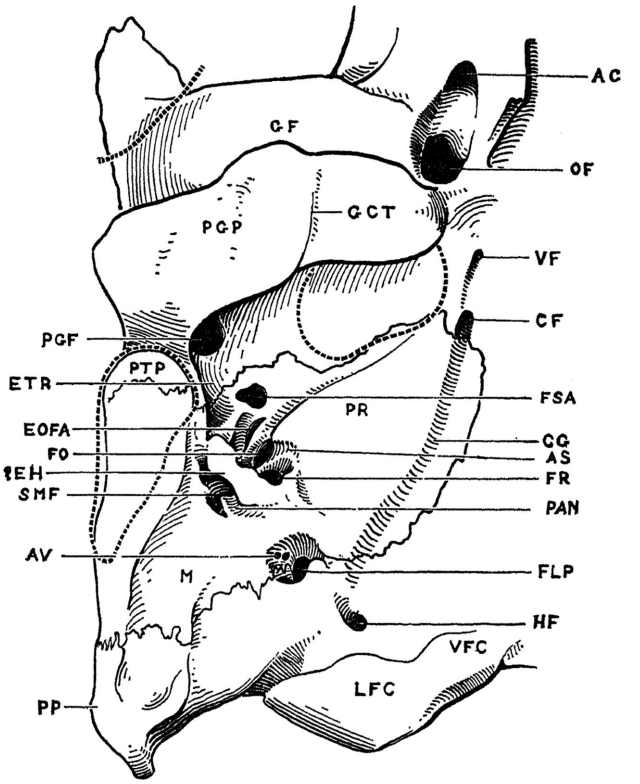

FIG. 24. Right ear region of *Apternodus*, based primarily on the type of *A. brevirostris*, but with missing parts (set off by dotted lines) drawn in from type of *A. gregoryi*. Abbreviations on page 129.

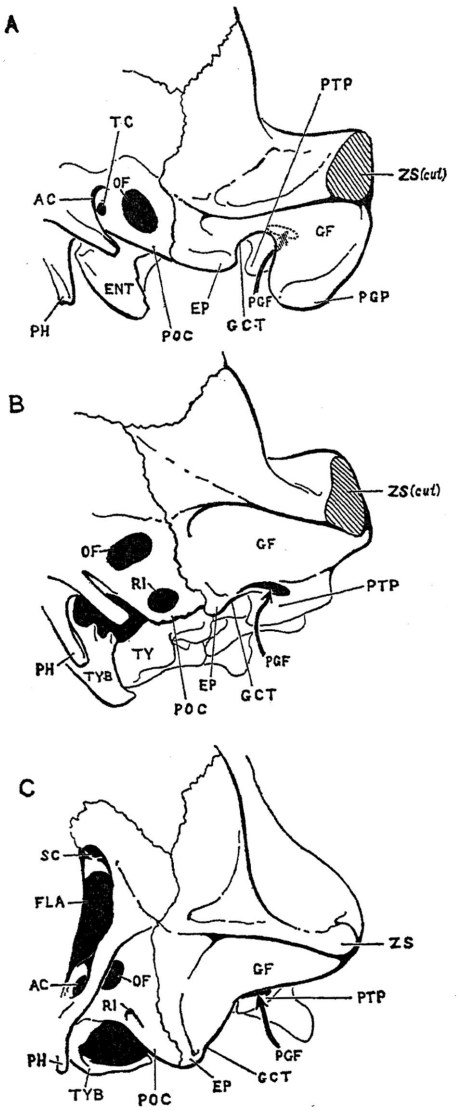

FIG. 25. Loss of processus postglenoideus and its functional replacement by the entoglenoid process in the Lipotyphla. A. Direct anterior view of glenoid fossa of Oligocene leptictid "*Ictops*," a member of the Menotyphla. Both entoglenoid process (EP) and true processus postglenoideus (PGP) present, the latter placed on zygoma lateral to braincase and anterolateral to postglenoid (venous) foramen (PGF). B. Corresponding view of *Erinaceus*, a primitive member of the Lipotyphla (Erinaceomorpha). True postglenoid process lost, while entoglenoid process, medial to postglenoid foramen, beneath braincase, and continuous with preotic crest of alisphenoid (POC), is yet small. C. Corresponding view of *Tenrec*, a lipotyphlan of the suborder Soricomorpha, with entoglenoid process enlarged to replace processus postglenoideus functionally. Other abbreviations on page 129.

foramen of *Apternodus* is less anomalous than that of the Lipotyphla in being posterior, rather than posterolateral, to the postglenoid process.

The orbito-temporal region is obscure, but from the American Museum skull (A.M.N.H. No. 22476) it can be determined that the maxilla forms little of the orbital wall, an important contrast to the Lipotyphla; it cannot be determined how far the palatine extends into the orbit. An alisphenoid canal is present, but (to judge from the American Museum skull) apparently no transverse (venous) canal. I have been unable to determine the presence or absence of a suboptic (or even the optic) foramen, but Schlaikjer (1933) does not describe one. A small ethmoid foramen is present, at least in the American Museum skull.

Although the lacrimal foramen of *Apternodus* is proportionately large, a resemblance to both *Solenodon* and *Nesophontes*, in one particular the lacrimal region of *Apternodus* is unlike that of the Lipotyphla, for its anterior rim is thick and torus-like, which suggests that a lacrimal tubercle is still present, although imperfectly (but perceptibly) distinct from the preorbital rim. Moreover, the canal, rather than running straight forward from the foramen as in *Solenodon* and *Nesophontes*, runs straight inward, then bends forward.

The infraorbital canal of *Apternodus* is more anteriorly placed than in the Lipotyphla, for its posterior orifice is opposite M^1, while in the Lipotyphla the posterior orifice is opposite M^2 or even more posterior. The anterior orifice in *Apternodus* is above P^3, the usual position in creodonts, condylarths, carnivores, and so on, and probably the primitive position. Save in the erinaceids related to *Galerix*, perhaps the most primitive of Lipotyphla, the foramen is forced to a level posterior to P^3 by the muscles of the proboscis and the labial vibrissal pad.

In addition to these features in which *Apternodus* differs from all Lipotyphla, *Apternodus* differs particularly from *Solenodon* in

numerous features, the most important of which are:

1. Absence of pyriform fenestra, as demonstrated most clearly by the Harvard skull.
2. Apparent presence of some sort of osseous bulla at the rostro-mesial corner of the middle ear. This statement is based on the presence in the type of *Oligoryctes*, a genus very closely related to *Apternodus*, of a natural cast of some bony bullar element in this region, as described by Hough (1956). Just what element left this impression is doubtful, but whatever it was, it represented a marked departure from *Solenodon*, for in the latter genus the middle ear is quite open in this region, defined only by the tubal cartilage, with no alizarin-staining element, much less a well-developed bone.
3. Absence of the condyloid canal adjacent to the foramen magnum, as determined on the American Museum specimen.
4. No indication of division of the capitular facets of the glenoid fossa, as determined in both the Harvard and American Museum specimens.
5. Form and position of infraorbital canal (determined on both the Harvard and American Museum specimens). In *Apternodus* the canal lies over the rear of P^3, the whole of P^4, and the anterior portion of M^1, whereas the canal of *Solenodon* lies over M^1. In *Solenodon* the canal is of cylindrical caliber, but in *Apternodus* the canal is of much greater vertical than horizontal diameter, with slit-like, rather than circular, anterior orifice.
6. The mental foramen of *Apternodus* lies beneath P_3, rather than the rear of P_4 or the front of M_1, as in *Nesophontes* and *Solenodon*, and the Lipotyphla in general, the Erinaceidae excepted.
7. Root of enlarged upper incisor extending upward and *backward* into wall of muzzle, rather than upward and forward into margin of naris.

We may say, in short, that the skull of *Apternodus* shows no resemblance to that of *Solenodon* that is not seen in *Nesophontes*, while showing important differences, not only from that of *Solenodon*, but from that of all the Lipotyphla.

General Remarks on the Comparison of *Solenodon* with *Apternodus*

It seems safe to say that if *Apternodus* did not have zalambdodont teeth, the suggestion that it is related to *Solenodon* would never have been made. Some features, such as the weak orbital wing of the maxilla, true postglenoid process, and mesial entocarotid artery rather than arteria promontorii, argue that *Apternodus* (and the probably closely related *Oligoryctes*) is not closely related to the Lipotyphla.

The peculiar plate-like developments of the auditory-temporal region seem quite unique to *Apternodus*, although the large size of the epitympanic recess associated with these plates recalls the condition in the Chrysochloridae (an obviously analogous, rather than homologous, condition, for the resemblance is not at all detailed). In the chrysochlorids the inflated epitympanic region is associated with enlargement of the malleus, and perhaps similar modification explains the condition in *Apternodus* (and *Oligoryctes*). The epoicotherids of the Palaeanodonta also show inflation of the epitympanic region to a remarkable degree, particularly in *Xenocranium* (see Colbert, 1942), but here again the resemblance appears to be merely analogous.

The posterior portion of the auditory plate of *Apternodus* is quite different from that of the epoicotherids or chrysochlorids, for it is a large, wing-like structure formed by the conjoined paroccipital (jugular) process of the exoccipital, the mastoid process of the petrosal, and the post-tympanic process of the squamosal. None of the Lipotyphla or Menotyphla (Tupaiidae, Leptictidae, Macroscelididae) shows indication of conjunction of these processes, but some of the creodonts, particularly the Oxyaenidae, show the development of these processes from a short but massive common pedicle, forming a sort of handle at the postero-latero-ventral "corner" of the skull. Inflation of the epitympanic recess in conjunction with this handle-like, paroccipital-mastoid-post-tympanic process might lead to the formation of a temporal plate like that of *Apternodus*.

In the foregoing comparison it is stated that no vestige exists in *Apternodus* of the zygomatic roots of the maxilla and squamosal, for there is no trace of the pointed processes seen in *Solenodon*, vestiges of a thin, rod-like, lipotyphlan zygoma. Possibly, however, the nearly vertical rim-like keel on the anterior (squamosal) portion of the temporal-auditory plate and the long diagonal ridge on the maxilla (running from above the infraorbital foramen to the outer alveolar wall of M^1) may represent vestiges of a vertically deep, creodont type of zygoma.

TABLE 1

SKULL OF *Apternodus* CONTRASTED WITH THAT OF *Solenodon* AND *Nesophontes*

	Apternodus (and *Oligoryctes*)	*Solenodon* and *Nesophontes*
Internal carotid	Runs mesial to middle ear	Runs through middle ear as arteria promontorii
Stapedial artery	Enters skull through discrete foramen in petromastoid	Enters skull by pyriform fenestra
Tympanic process of petrosal	(?) Represented by spine that meets mastoid to surround stylomastoid foramen	Tab-like, not meeting mastoid
Pyriform fenestra	Absent	Present, nearly eliminating alisphenoid and squamosal from roof of middle ear
Epitympanic recess	Abnormally large	Abnormally small
Paroccipital, mastoid, and post-tympanic processes	Joined to form an expanded plate	Independent, no plate formed
Bulla	Ossified at anteromedial corner of middle ear, as indicated by natural cast in *Oligoryctes*	None formed
Posterior lacerate foramen	Restricted to a small, oval opening by a wing of petrosal	Continued as a slit far forward between petrosal and basioccipital, exposing inferior petrosal sinus
Condyloid canal opening at foramen magnum	Absent	Present
Postglenoid process	A true processus postglenoideus	A modified entoglenoid process
Capitular facet of glenoid fossa	Simple	Double
Vestige of squamosal root of zygoma	Absent, unless represented by a vertical crest	A pointed subcylindrical spine
Tympanic wing of basisphenoid	Absent, at least (*Oligoryctes*) adjacent to tubal cartilage	Indicated by vestigial crest mesial to tubal cartilage
Orbital wing of maxilla	Small, elongate-rectangular, confined to lower portion of orbit	Large, semicircular, forming major part of orbital wall
Cribriform plate	Far back, between glenoid articulations (*fide* Harvard skull)	Well anterior to glenoid region (more anterior in *Solenodon* than in *Nesophontes*)
Postglenoid foramen	In epitympanic recess	External to epitympanic recess
Ventral facets of occipital condyles	Small, pointed mesially, widely separated	Large, rounded mesially, approximated
Lateral facets of occipital condyles	Extending dorsally nearly to level of top of foramen magnum	Falling far short of level of top of foramen magnum
Foramen magnum	Much wider than high	Much higher than wide
Occiput	Very broad, concave from side to side	Narrow, convex from side to side
Foramen Vesalii of transverse canal	Absent	Present
Temporalis origin	Not extending over orbit	Extending over orbit
Lacrimal canal	Extending inward from foramen, then bending forward	Extending forward from foramen
Lacrimal tubercle	Present	Absent
Root of enlarged upper incisor	Directed upward and strongly backward	Directed upward
Vestige of maxillary root of zygoma	Absent, unless represented by a diagonal crest that is flexed forward	Pointed, directed backward

This is, of course, pure conjecture, and in the absence of more concrete evidence further discussion of this point is idle. Still, the auditory carotid pattern, glenoid fossa, postfrontal process, and weak orbital wing of the maxilla are decidedly more in keeping with creodont relationships for *Apternodus* than with affinity to the Lipotyphla.

Again we must return to the teeth and the supposed importance of zalambdodonty. Two views of the morphological significance of zalambdodonty have been expressed. One view holds that the living zalambdodonts show a secondary simplification of the teeth, but such a morphological innovation is so peculiar that those forms possessing zalambdodont dentition are probably related. Such a view appears in such works as Gregory (1910), Matthew (1913), and Simpson (1928). Another view holds that the zalambdodont dentition is derived directly from the rather similar dentition of some Mesozoic mammals and thus is indicative of a very ancient separation of mammalian stocks. Such a view is implicit in Hough's (1956) assertion that the zalambdodont molar is the simplest modification of the reptilian cone, and is most explicitly stated by Butler (1939), that the zalambdodonts have possible affinity with the Paurodontidae, are not closely related to other insectivores, and share with the Didelphidae and the monotremes the distinction of being the most primitive of living mammals.

[It must be noted that Butler in 1956 dropped this view entirely and independently came to conclusions basically similar to those of the present author, that the zalambdodonts are related more or less closely to the moles and shrews. Indeed, after a first draft of the present paper had been completed, I was surprised to see a letter from Butler in which he, again independently, suggested the possibility of close relationship between *Solenodon* and *Nesophontes*. It should be stated here, however, that while the conclusions of Dr. Butler and myself are independent in the sense that there was no communication between us during our separate researches, both of us came to our opinions from the study of similar material (the comparison of the skull of the Leptictidae with that of other insectivores).]

Both these views run into the difficulty that several groups of mammals demonstrably unrelated to the zalambdodont insectivores have acquired a zalambdodont dentition (in the sense that the upper molars have one main central cusp that dwarfs the other cusps by comparison). Some of these may be listed:

1. *Notoryctes*, the marsupial "mole" of Australia, while possessing all the distinctive features of the marsupials, shows a perfectly zalambdodont dentition, which bears perhaps greater resemblance to that of *Apternodus* than does the dentition of *Solenodon*.

2. The South American marsupials related to *Borhyaena* show a single main buccal cusp of the upper molars which thus have a zalambdodont pattern. Here, however, it appears to be the metacone that is hypertrophied, to judge from *Prothylacinus*. It should be noted that the borhyaenines appear to be independent in their zalambdodonty not only of the placental zalambdodonts but of *Notoryctes*, the latter being a modified dasyurid, while the borhyaenines show no clear relationship to other marsupials (they have no alisphenoid bulla, otherwise characteristic of marsupials, for example).

3. The advanced Hyaenodontidae show a zalambdodont type of dentition which has arisen within the limits of that family. (See Osborn, 1907, p. 139, for a figure of the structural series leading from *Sinopa* to *Hyaenodon*.)

4. The aberrant Santa Cruz mammal *Necrolestes* shows triangular molars, often interpreted as zalambdodont. The affinities of *Necrolestes* are questionable. Scott (1903–1905, pp. 379–381) regarded this genus as an insectivore related to *Chrysochloris*; Winge (1941, p. 217), as a marsupial; while Simpson (1927), although noncommittal, considered the possibility of chrysochlorid relationship. Relationship to the Xenarthra appears most likely to me, for the humerus and ulna are decidedly armadillo-like, while the postzygapophyses of the lumbar vertebrae are webbed together, the prezygapophyses are provided with short and blunt metapophyses, and the transverse processes are in contact with the adjacent posterior vertebra—all features of the zenarthran dorsal column. In addition, the Princeton Museum skull shows an element at the nasal orifice that appears to be

the nariale, an element that would be diagnostic of the Xenarthra were it not so easily lost through damage that few skulls are well enough preserved to be so diagnosed. The whole nostril region appears essentially similar to that of the dasypodid *Euphractus*. (See Wegner, 1951, for the most recent account of the nariale of Xenarthra.) *Necrolestes* is unusual in having large anterior upper incisors, those of the left and right side contiguous, whereas most Xenarthra have a wide gap at the front of the mouth between the incisors, probably for the passage of the tongue. However, the peculiar armadillo *Peltephilus* had contiguous, enlarged, anterior incisors and may have been related to *Necrolestes*.

The present author does not claim, however, that an identical tooth pattern has been developed in these various lines. Each has its own peculiarities. But no near identity in dental form exists between *Solenodon* and *Apternodus*. The abrupt change in size and complexity from P^4 to the tooth immediately anterior and the form of the buccal styles of the upper molars are very similar in *Solenodon* and *Nesophontes* and quite unlike *Apternodus*, while the similarity between Pd^4 of *Solenodon* and P^4 of *Nesophontes* is far greater than the match between any two cheek teeth of *Solenodon* and *Apternodus*.

Thus, the dental argument for affinity between *Apternodus* and *Solenodon* reduces to the importance to be attributed to one morphological feature of molar pattern, and even this supposed resemblance is doubtful, as the zalambdocone of *Solenodon* has a more lingual bite than that of *Apternodus* and is probably not homologous in the two genera. I would be inclined to put the resemblance of both genera to Mesozoic mammals in the same category with the similarity in molar form between the specialized bat *Harpionycteris* and the multituberculate *Ctenacodon*.

The skull, rather than arguing for close relationship between *Solenodon* and *Apternodus*, argues for the isolation of *Apternodus* from the Lipotyphla and suggests possible creodont affinities of the genus.

Of the continental fossil forms supposed to be related to *Solenodon*, there remain only the poorly known *Micropternodus* and *Clinopternodus*. These may be discussed briefly.

MICROPTERNODUS AND *CLINOPTERNODUS* COMPARED WITH *SOLENODON*

THE GENUS *Micropternodus* was described by Matthew (1903) from the Chadron of Montana, based on a lower jaw with teeth, but lacking most of the ascending ramus and the angular region. *Clinopternodus* was described by Clark (*in* Scott and Jepsen, 1936) under the (preoccupied) name *Clinodon*, from a lower jaw lacking both incisor region and the portion posterior to the first molar. It appears to represent *Micropternodus* in the Chadron of South Dakota, differing in larger size and more crowded dentition.

The very high trigonid and low talonid led Matthew to conclude that *Micropternodus* is a zalambdodont, and he noted the molars were somewhat like those of *Tenrec*.

Schlaikjer (1933) determined that P_2 of *Micropternodus* is two-rooted, rather than one-rooted as thought by Matthew, and noted the following resemblances to *Solenodon*: dental formula $_{3-1-3-3}$; I_2 larger than either I_3 or I_1; P_2 (the most anterior) two-rooted; anteroposterior ridge of talonid confluent with base of trigonid; general shape of the mandible; and position of anterior base of coronoid process. From these resemblances, Schlaikjer concluded that *Micropternodus* is closely related to *Solenodon* and should be placed in the Solenodontinae.

It must be noted that no one of these features is sufficiently unusual to be definite evidence of relationship. Resemblances 1 and 3 must be considered together, for P_2 is not actually present and is represented only by alveoli. Thus, it is possible that actually two single-rooted premolars were present, rather than one double-rooted tooth. *Clinopternodus* has only three premolars, but the most anterior premolar is single-rooted. Resemblance 2 is not so great in fact as it appears in wording, for the incisors (represented only by alveoli) are much less unequal in *Micropternodus* than in *Solenodon*. Character 4 is actually a difference from *Solenodon*, not a resemblance, for in *Micropternodus* the anteroposterior talonid crest (crista obliqua) is joined to the base of the metaconid, whereas in *Solenodon* the crista obliqua joins the base of the protoconid rather far buccally. Features 5 and 6 appear to be parts of one resemblance, and this resemblance is far from detailed.

Thus, in *Micropternodus* the symphysis is produced posteriorly into a slight projection that forms a definite irregularity in the ventral profile of the jaw, whereas the symphysis in *Solenodon* is in the same plane, and continuous, with the ventral profile of the jaw. *Solenodon* has multiple mental foramina, the most posterior of which is usually beneath M_1, occasionally beneath P_4, all in conformity with lipotyphlan affinities. But in *Micropternodus* there is but a single foramen placed beneath the rear of P_2 and front of P_3.

The dentition of *Micropternodus* and *Clinopternodus* does not by any means prove tenrecid or solenodontid affinities, for the hypoconid, although low in proportion to the trigonid, is quite distinct and salient, which suggests that it occluded between well-developed paracones and metacones (i.e., the upper dentition was dilambdodont). The form of the trigonids is not like that seen in *Solenodon*, for the paraconid is more anteriorly produced and is separated from the metaconid by a vertical groove on the lingual surface of the trigonid. Perhaps the most nearly similar lower molars are those of the middle Eocene nyctitheriid *Myolestes*. The high canine is also quite unlike *Solenodon*, although suggested in *Nesophontes*.

Because what little is known of *Micropternodus* and *Clinopternodus* shows no unusual resemblance to *Solenodon* and does not even favor "zalambdodont" affinities (the chief reason for suggestion of relationship to *Solenodon*), it seems best to remove these genera from the Solenodontidae and refer them to the Nyctitheriidae, the family to which *Myolestes* is referred.

NOTES ON *PALAEORYCTES*

IN 1913 MATTHEW DESCRIBED a small placental skull from the Puerco "basal Eocene" (=Palaeocene) as a zalambdodont insectivore. This form, *Palaeoryctes puercensis*, would be the earliest known zalambdodont, and for this reason much interest attaches to it in the study of zalambdodont relationships.

The specimen (A.M.N.H. No. 15923) consists of the palate without premaxillae or canine alveoli; the upper molars and premolars; the base of the skull without occipital condyles or glenoid-zygomatic regions; the right dentary with the posterior five teeth, but without anterior, coronoid, condylar, or angular regions; the left dentary with canine alveolus and postcanine dentition, but lacking the ascending ramus and incisive-symphyseal region; and a considerable portion of the left side of the axis. Fragmentary as the material is, it still constitutes one of the best specimens of a small Palaeocene mammal. To the present author's knowledge, no additional material of *Palaeoryctes* has been described since.

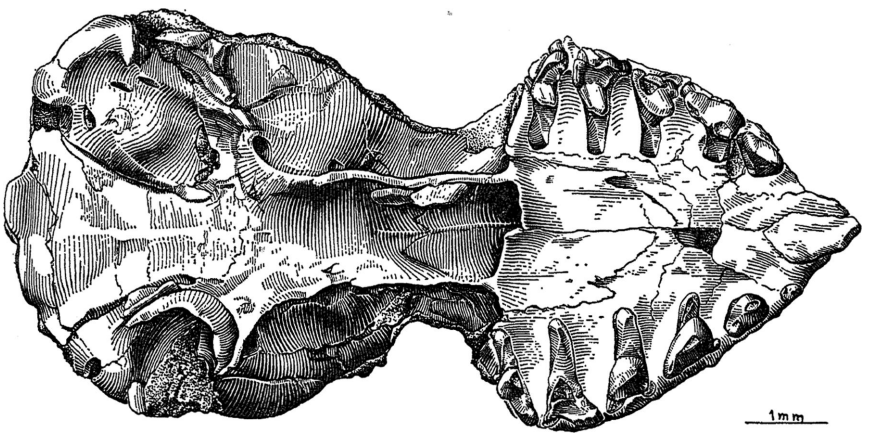

FIG. 26. *Palaeoryctes puercensis*. Ventral view of the skull without correction for breakage or distortion.

The dentition of *Palaeoryctes* is the sole evidence for relationship to living zalambdodonts, for, as Matthew himself remarks, "the basicranial structure appears to be more primitive and is more nearly in accord with that of the early Creodonts." The same may be said with regard to the (undescribed) fragment of the axis, which shows a heavier and more wing-like transverse process of more elevated position relative to the vertebrarterial canal than seen in any lipotyphlan, living zalambdodonts included, and much more like that of the Menotyphla and creodonts.

But even the teeth of *Palaeoryctes* differ considerably from those of any living zalambdodont. The "zalambdocone" of *Palaeoryctes* is plainly a joined paracone and metacone, with the apices of these cusps still distinct although closely crowded, while a well-developed protocone extends far linguad from the "zalambdocone" as a narrow and strap-like, lingual heel. As a result, the "zalambdocone" is located at about the midpoint of the buccolingual diameter of the upper molar. This is in contrast to the molar form of the living Tenrecoidea (*sensu* Simpson) in which the "zalambdocone" lies either near or on the lingual border of the tooth, and the protocone (if the lingual cingulum be so interpreted) is either absent (Tenrecinae) or a mere semilunar shelf that does not come into contact with the lower molars when the jaws are closed. In all "Tenrecoidea" but one of the two species of *Potomogale* (*P. velox*) the cusp is simple, while in *Potamogale velox* the subsidiary cusp, often interpreted as a metacone, is more

lingual than that of *Palaeoryctes* and much more widely separated from the main "zalambdocone" cusp (it lies about halfway between the metastyle and the "zalambdocone").

Previous to Matthew's description of *Palaeoryctes* much informed opinion (e.g., Gregory, Osborn, and Leche) had held that the "zalambdocone" of living zalambdodonts represented the protocone of the normal tribosphenic molar. As the "zalambdocone" of *Palaeoryctes* is obviously the conjoined paracone and metacone, Matthew argued that such must also be true of the "zalambdocone" of living zalambdodonts. This argument has been accepted at face value by most subsequent workers, and *Palaeoryctes* has been cited as the fossil evidence that (1) the zalambdodont dentition is a very ancient one, and (2) the "zalambdocone" of living zalambdodonts is essentially the paracone.

But Matthew's argument does not bear close inspection, for it appears to reduce to the following:

1. He has a very ancient skull and dentition which he chooses to refer to the living zalambdodonts.
2. This reference is based on similarity of teeth.
3. The teeth are different from those of living zalambdodonts and cause him to question the interpretation of cusp homologies.
4. The associated basicranium shows no great resemblance to that of living zalambdodonts, but resembles that of creodonts.

In truth, Matthew appears to have identified *Palaeoryctes* as a zalambdodont, because this seemed a solution to a zoogeographic puzzle. Indeed, Matthew's opening remarks are on the geographical distribution of zalambdodonts. As he did not question the monophyletic origin of the group, or the affinity of *Solenodon* to the African and Madagascan forms, only two solutions presented themselves to him: (1) former occurrence of zalambdodonts in the Nearctic and Palaearctic regions, with the present-day forms showing a relict distribution; or (2) a land bridge from Africa to the West Indies. As not a shred of geological evidence favors the latter explanation, the existence of a primitive zalambdodont in the Palaeocene of New Mexico appeared most welcome evidence for the relict-distribution hypothesis and fitted the facts as then known. Because *Nesophontes* had not yet been discovered, Matthew was, of course, unaware that his interpretation would later pose an even greater problem: why the two West Indian genera of Insectivora, supposedly representing evolutionary lines distinct since the early Palaeocene, should be so remarkably similar in cranial details, as well as some details of dentition, such as the buccal-stylar region of the molars.

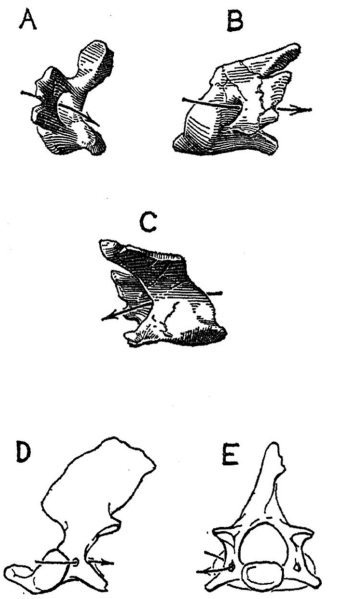

FIG. 27. Axis of *Palaeoryctes* compared with that of a lipotyphlan, *Solenodon paradoxus*. (Not to same scale.) Arrow passes caudad through the vertebrarterial canal. A. Fragment of the axis of *Palaeoryctes*, posterior view. B. Same, lateral view. C. Same, medial view. D. *Solenodon*, lateral view. E. Same, posterior view.

A further difficulty is presented by the lack of basicranial resemblance between *Palaeoryctes* and living insectivores. Living zalambdodonts agree in basicranial details with the Erinaceidae, Talpidae, and Soricidae, whereas these features are not observed in *Palaeoryctes*. If *Palaeoryctes* is really a primitive zalambdodont, then this would imply that the zalambdodont basicranial structure has paralleled that of dilambdodont lipotyphlans. As the resemblance in basicranial features among lipotyphlans (including "zalambdodont" forms) is more detailed than

the dental resemblance between *Palaeoryctes* and living zalambdodonts, it appears more probable that the parallelism has been in the dentition and that the dental affinity between *Palaeoryctes* and the zalambdodonts is spurious.

The promontorium of *Palaeoryctes* is quite smooth and devoid of grooves for the carotid

other common features emphasizing the probable naturalness of the group.

Whereas in the Lipotyphla the fenestra rotunda opens into a pit behind the promontorium, in *Palaeoryctes* the fenestra opens directly on the rear surface of the promontorium. In the Lipotyphla a process of the promontorium, behind the pit for the fenestra ro-

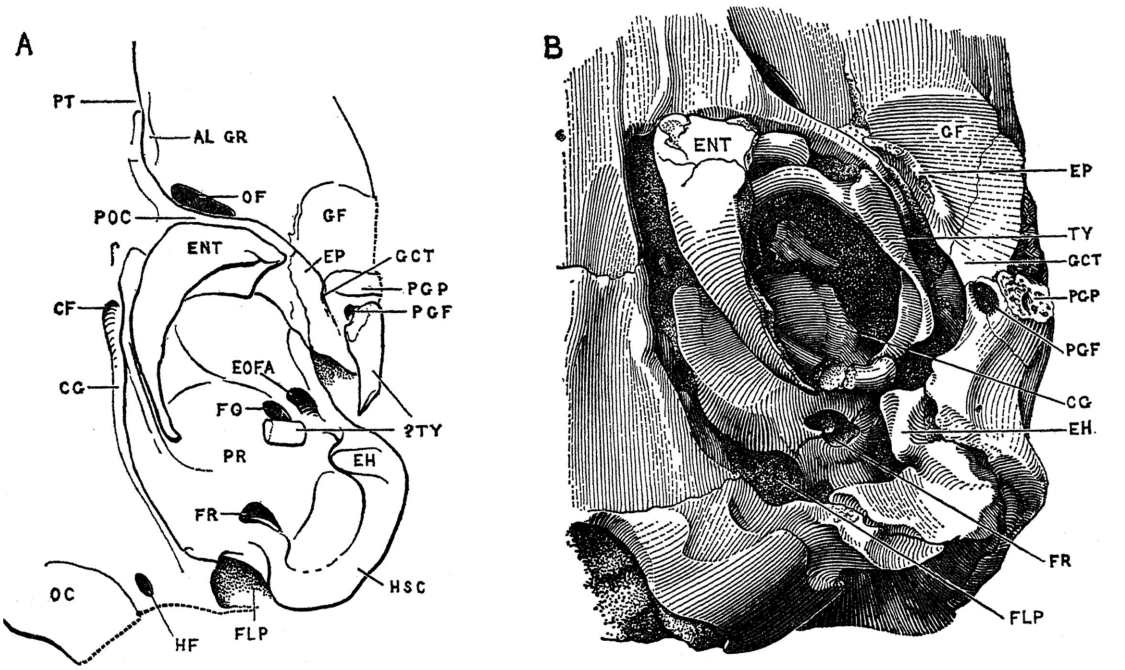

FIG. 28. Auditory region of *Palaeoryctes* compared with that of the Oligocene liptictid "*Ictops*" (Order Menotyphla), not to same scale. A. *Palaeoryctes*, combined from both right and left sides of the unique specimen shown in figure 26. B. "*Ictops*" (C.N.H.M. No. HM 14), without correction for crushing or distortion. Abbreviations on page 129.

arterial circulation, and no groove for an arteria stapedia crosses the fenestra ovalis, so that the latter does not lie in a fossa. Instead, the stapedial artery appears to be absent, and the main entocarotid runs in a groove mesial to the petrosal, as in the creodonts (and *Apternodus*). This is quite unlike the lipotyphlan arterial pattern, in which the carotid enters the middle ear to branch on the promontorium into an arteria stapedia and an arteria promontorii. As Butler (1956) has indicated, this carotid pattern appears to be of considerable importance in higher taxonomy and characterizes a cluster of placental orders (the Lipotyphla, Menotyphla, Dermoptera, and Primates), orders that have a host of

tunda, extends downward and forward to aid in the support of the tympanic. This process is strongest in the Soricidae, *Solenodon*, *Nesophontes*, and *Potamogale*, and weakest in *Tenrec*, in which it is very feeble in skulls that are not fully mature. No trace of this process is to be seen in *Palaeoryctes*.

On the left side a bullar bone is preserved in *Palaeoryctes*, lying at the rostromedial corner of the tympanic cavity, in the form of a hollowed-out crescent. Matthew identified the bone as the tympanic, although he noted that it is abnormally mesial in position for a tympanic. However, the bone is more similar in both form and position to the entotympanic of leptictids (a bone that Matthew mis-

took for the tympanic in "*Ictops*" *bullatus*). In the Lipotyphla the entotympanic is absent. A fragment on the left promontorium and another behind the right postglenoid foramen in *Palaeoryctes* suggest in both form and position the corresponding parts of the tympanic of "*Ictops*."

On the right side in *Palaeoryctes* there remains the mesial portion of a small, true, postglenoid process, set off from the entoglenoid process by a notch. As outlined above, the postglenoid process of those lipotyphlans in which it is suggested at all appears to be the modified entoglenoid process, not homologous with the postglenoid process of other mammals. The glenoid fossa is largely broken off on the right side, completely missing on the left. This in itself speaks against relationship to the lipotyphlans, for the latter have the jaw articulation essentially anterior to the ear, rather than lateral and anterior to it, so that it might be expected that the glenoid surfaces would appear on the portions of the squamosals preserved in *Palaeoryctes*.

As Matthew notes, in *Palaeoryctes* "the alisphenoid canal was apparently not present, a deep groove, incompletely bridged for a short distance, occupying its place." This is decidedly unlike most Lipotyphla (except some specimens of *Echinosorex*) in which the canal exists as a foramen in the alisphenoid boring directly into the chamber for the Gasserian ganglion, permitting entry of the ramus inferior of the stapedial artery. The foramen in the Lipotyphla (except some Erinaceidae) can, in fact, hardly be called a canal, for it is not a bony tube for the artery alone, with lateral and mesial bony walls. It is, rather, a simple hole, without any mesial bony wall to separate it from the Gasserian fossa, while its lateral bony wall is really but the external wall of the Gasserian fossa. The condition seen in *Palaeoryctes* is that seen in the Menotyphla, creodonts, and carnivores, in which the internal maxillary artery lies in a groove on the external surface of the bony lateral wall of the Gasserian fossa and is more or less protected externally by a thin, sometimes incomplete, bridge of bone, thus forming a bony tube for the artery alone.

Even the general form of the skull in *Palaeoryctes* appears to speak against affinity with modern zalambdodonts, for it is strongly constricted a short distance posterior to the level of the rear of the false palate. In modern zalambdodonts this portion of the skull houses a large ethmoid complex, so is not greatly, if at all, narrowed.

Palaeoryctes is from the early Palaeocene, and no intermediate fossil forms are described to link this genus with living forms. In the absence of any support from cranial anatomy or the fragmentary axis, it is solely the teeth that argue for any relationship to modern zalambdodonts, while even here the argument is weak in the absence of any degree of detail in the resemblance. Although *Palaeoryctes* is a fossil, the argument for its relationships fits the discipline of classical comparative anatomy rather than of paleontology, in the absence of a chain of intermediate forms from intermediate time levels. By the standards of comparative anatomy the argument for zalambdodont affinities fails, for it cannot be shown that the zalambdodonts are more similar to *Palaeoryctes* than to other forms.

What has been demonstrated by *Palaeoryctes* is that the paracone and metacone may be closely joined, but this had already been demonstrated by the series within the Hyaenodontidae from *Sinopa* to *Pterodon*. There is no evidence that this has direct bearing on the problem of origin of the living zalambdodonts.

Much has been made of a supposed resemblance between the molars of *Palaeoryctes* and those of the West African otter-shrew *Potamogale velox*, and the latter was cited by Matthew as a dental intermediate between *Palaeoryctes* and the modern "Tenrecoidea." In *P. velox* there is an additional cusp posterior and buccal to the "zalambdocone" which has been homologized with the metacone, while the "zalambdocone" of *P. velox* has been identified as the paracone. By this interpretation *Potamogale velox* would have the most primitive dentition of zalambdodonts and would retain distinctness of paracone and metacone from a *Palaeoryctes*-like ancestor (presupposing homology of the zalambdocone of modern zalambdodonts with a fused paracone and metacone). Indeed, because the "paracone" and "metacone" of *Potamogale velox* are more widely separated than in *Palaeoryctes*, an even more ancient ancestry might be suggested.

Now, there is nothing else about *Potamogale* to suggest that it is a primitive zalambdodont. It is highly specialized as an aquatic form, with an oar-like tail, cornified valvular nostrils, syndactylous second and third toes, greatly reduced gall bladder, totally reduced clavicles and lacrimal bone, and a closed bulla formed in part by a large triangular lobe arising from the tympanohyal. All these specialized features cause some suspicion of a theory of dental evolution that makes *Potamogale* the most primitive of modern zalambdodonts. But it is still possible that *Potamogale* has specialized in the majority of its features but retained dentitional characters from a primitive ancestral form. On this theory more primitive forms related to *Potamogale velox* might be expected to retain the *Palaeoryctes*-like features in dentition but show fewer specializations in general structure.

Such, however, does not appear to be the case. Recently two species of potamogalines have been discovered living in West Africa: *Potamogale ruwenzorii* (De Witte and Frechkop, 1955), from the Ruwenzori region, eastern Congo; and *Micropotamogale lamottei* (Heim de Balzac, 1954; and Heim de Balzac *in* Grassé, 1955, pp. 1665–1667), from the French Cameroons. These forms show close relationship to *Potamogale* in skull structure, including the closed bulla, and in syndactylous toes, but show a more primitive phyletic position by lack of oar-like specialization of the tail, small size (about half of that of *P. velox*), and normal nostrils. The most important feature of both these forms, however, is the dentition; both *Micropotamogale* and *Potamogale ruwenzorii* have a simple zalambdocone without any indication of the "metacone" of *Potamogale velox*. The dentition in both the small potamogalines is, in fact, essentially as in *Microgale* and *Geogale*, Malagasy forms related to the Potamogalinae. Thus it would appear that the "metacone" of *Potamogale velox* is not a heritage from a *Palaeoryctes*-like ancestor, but more likely a neomorphic structure that has arisen within the genus, perhaps as an adaptation to the crab-eating habits of the otter-shrew.

Palaeoryctes, to summarize, shows nothing in its teeth to indicate special affinity to living zalambdodonts, while its basicranial structure is a strong argument against such affinity. Similarly the axis speaks against affinity with modern insectivores.

When we turn to the question of what *Palaeoryctes* is, after seeing what it is not, the dental resemblance between *Palaeoryctes* and *Deltatheridium* pointed out by Simpson (1928) seems real. Indeed, the resemblance between *Palaeoryctes* and *Deltatheridium* appears to me to be greater than the similarity between the latter and *Didelphodus* and its relatives. If the Didelphodontinae are properly included in the Deltatheridiidae, as there is every reason to believe, then it would appear to me inconsistent to leave *Palaeoryctes* out of this assemblage. (The single known upper molar of *Gelastops* is quite similar to the corresponding tooth of *Palaeoryctes*.) The argument for the present must rest on close dental resemblance, for the parts of the skull preserved in *Palaeoryctes* are almost precisely those missing in known specimens of the Deltatheridiidae of Simpson's (1945) classification.

A minor inconvenience results from following the present suggestion to merge the families Palaeoryctidae and Deltatheridiidae; the family name Palaeoryctidae, being older, must take precedence over the name Deltatheridiidae, a name made famous by the antiquity of its type genus.

It must be confessed that in view of our lack of definite knowledge of the affinities of Simpson's Deltatheridiidae, assertions of relationship of that group to *Palaeoryctes* say very little about the ancestry and descendants of the latter genus. Still, such an assertion is offered here as a hope that a common solution exists to the problem of *Palaeoryctes* and the problem of *Deltatheridium*. It may be well to point out that the carotid circulation in the ear of *Apternodus* appears to be essentially similar to that of *Palaeoryctes* and that the general proportions of the facial region are similar in *Didelphodus* and *Apternodus*.

We have now discussed various fossil genera, sometimes regarded as related to *Solenodon* but apparently not even members of the same order of mammals. We may now turn to the discussion of certain lipotyphlan groups that have been suggested as close relatives of the West Indian insectivores.

THE POSITION OF THE ANTILLEAN INSECTIVORES AMONG THE LIPOTYPHLA

As indicated by Butler (1956), the Lipotyphla form a closely knit and natural group, the differences between the families being largely in detail. In addition to the Antillean genera, the order includes the following families: Erinaceidae, Talpidae, Tenrecidae (including Potamogalidae), Chrysochloridae, and Soricidae. An additional family, the Dimylidae, from the Oligocene and Miocene of Europe, is known almost entirely from teeth, and its affinities to the Lipotyphla are not proved. However, the resemblance of the Dimylidae to the Erinaceidae and Talpidae is so great that lipotyphlan affinity is very probable. The Lipotyphla thus correspond essentially to the Euinsectivora and Chrysochloroidea of Grassé (1955).

Of these families, the Soricidae appear to be the one family most closely allied to both *Solenodon* and *Nesophontes*. The close similarity between *Nesophontes* and the Soricidae was noted by Anthony (1916), who regarded the Nesophontidae as most closely related to the Soricidae. G. M. Allen (1917) noted even closer resemblance between *Nesophontes* and *Solenodon* and, as he did not question the tenrecid affinities of *Solenodon*, felt forced to deny soricid relationships of *Nesophontes* and to ally the genus with the Tenrecoidea. Anthony (1925) replied to Allen by citing cranial features in which *Nesophontes* differs from most Tenrecoidea and resembles shrews.

The real basis of this disagreement may be traced to the acceptance by both Allen and Anthony of tenrecid affinities of *Solenodon*. The possibility that *Solenodon* itself might be closer to shrews than to the Afro-Malagasy tenrecoids apparently was not considered by either Allen or Anthony, although it resolves the argument between these two authors. Anthony (1925) assumed that paleontology has "proved" the great antiquity of the "zalambdodont" dentition. This "proof," however, is based entirely on *Palaeoryctes* and *Apternodus*, and, as detailed in preceding sections, the cranial structure of these fossils makes it quite unlikely that they have anything to do with living "zalambdodonts."

Yet many features of the anatomy, development, and behavior of *Solenodon* indicate closer relationship to shrews than to the Tenrecidae (see table 2):

1. Absence of a basisphenoid bulla.
2. Structure of the roof of the middle ear, with large pyriform fenestra, very small epitympanic recess, and virtually no participation of the squamosal.
3. Absence of a foramen for the ramus inferior of the stapedial artery.
4. Tympanohyal dorsal in plane to the tympanic. (The Soricidae differ from both *Solenodon* and *Nesophontes* in having a large tympanohyal that meets the promontorium to support the tympanic, but the shrews are more like the Antillean genera than are the tenrecids in that the tympanohyal is dorsal to the tympanic.)
5. Strongly developed postpalatine torus.
6. Failure of the maxilla to extend backward along the pterygoid lamina.
7. Presence of two separate capitular cartilages in the glenoid fossa. [This is a feature apparently confined to shrews and the Antillean insectivores. The double dentary-squamosal articulation makes for a ginglymous joint insuring accuracy of occlusion in a rapid, snapping bite. I am inclined to regard this as a more specialized condition than that in the Tenrecidae, in which there is a single capitular cartilage, but it is possible that it is actually more primitive. The postglenoid process of the Tenrecidae, Soricidae, and Antillean insectivores does not appear to be homologous with the postglenoid process of other mammals but is, rather, a modified entoglenoid process—a process normally without connection to the mandibular joint and without capitular cartilage. Conceivably, then, the more medial "postglenoid" cartilage arose first as a separate neomorphic structure (essentially in the condition seen in *Solenodon*) which subsequently fused with the primitive (lateral) cartilage. Against this, however, is the observed trend in evolution of the capitular facets of the dentary. In the most specialized of modern shrews, such as *Neomys*, the capitular facets of the dentary are widely separated and mounted on what appear to be two quite independent condyles. In the less specialized modern genera, such as *Sorex*, *Crocidura*, and *Myosorex*, the capitular facets are separate but mounted on an undivided condyle. In the Oligocene soricid *Domnina* (determined on A.M.N.H. No. 32647, the type of *D. thompsoni*) the capitular facets are only partially separated. Indeed, the dentary condyle of *Domnina thomp-*

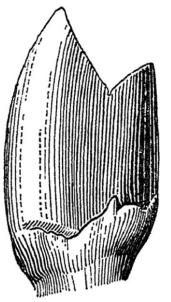

FIG. 29. Unworn first lower left molar of *Solenodon paradoxus*, seen from behind.

soni is nearly identical, except in size, with that of *Solenodon*. Thus, as the evolutionary trend in the dentary is towards division of a widened capitular facet, it seems likely that the trend in the squamosal followed a parallel course.]

8. Backward, rather than upward, development of the nuchal crest.

9. Foramen of sinus canal opening separately dorsal to the foramen lacerum anterius.

10. Anterior border of nasals transverse.

11. Presence of a lingually displaced hypoconulid adjacent to an entoconid. In the unworn lower molars of *Solenodon* (see fig. 29) the talonid bears at its linguo-caudal corner a bifid process not to be seen in the Tenrecidae or Chrysochloridae. The bifid process is similar to the characteristic juxtaposed entoconid and lingually displaced hypoconulid seen in the Soricidae and *Nesophontes*.

12. Abrupt change in complexity of upper cheek teeth at P^4. In *Solenodon*, as in the shrews and most Lipotyphla, P^4 is large and complicated, more or less like the molars, while the cheek teeth anterior to P^4 are abruptly smaller and simply conical in form. In the Tenrecidae and Chrysochloridae the change occurs more gradually and more anteriorly at P^3. In the Tenrecidae and Chrysochloridae it is P^3 that resembles Pd^4 of *Solenodon* and P^4 of *Nesophontes*.

13. Presence of lateral glands. These glands, first described by G. M. Allen (1910), were more thoroughly investigated by Mohr (1936b). They are otherwise characteristic of the Soricidae; indeed, Mohr's account begins with the phrase, "*Wie andere Soriciden hat auch* Solenodon *Seitendrüsen.*" As Mohr does not elsewhere discuss the taxonomic position of *Solenodon*, it is impossible to say whether this is a *lapsus* or a reference of *Solenodon* to the Soricidae. These glands are particularly prominent in the rutting season and show greater degeneration in non-rutting females than males, all quite as in Soricidae. These glands perhaps vary inversely with the anal glands, for, while well-defined and large anal glands are present in the Tenrecidae, as in the Erinaceidae and the Talpidae, these glands are excessively minute and diffuse in the Soricidae and have not been found by macroscopic examination in *Solenodon*.

14. Form of the snout. As in soricids, the upper lips of *Solenodon* are not joined to the snout by a frenum; instead, the right and left upper lips are separated by a cleft. When the two upper lips are pushed aside, no frenal membrane is to be seen, but only the epithelial investment of the proboscis cartilage. The nostrils of *Solenodon*, as in shrews, are longitudinally crescentic. In the Tenrecidae the upper lips are joined to a frenum, and the nostrils are round (although a deep alar groove may disguise this roundness to hasty examination).

15. Presence of a conus inguinalis in the male genital tract. The Tenrecidae and Chrysochloridae differ from other Lipotyphla in the absence of the conus, whereas *Solenodon*, as do shrews, moles, and erinaceids, possesses this structure.

16. Structure of the fetal membranes. Wislocki (1940) has reported on a fetus of *Solenodon paradoxus* and found great resemblance in placental structure to the Soricidae and no indication of tenrecid relationships. Thus, the allantoic vesicle is greatly reduced, as in shrews, rather than enlarged as in the Tenrecidae, while the yolk sac is very large and reflected as in shrews.

17. "Chattering." *Solenodon*, like the soricids, has the peculiar habit of constantly emitting an explosive sniffing sound (G. M. Allen, 1910; Mohr, 1936a). This is a peculiarity of behavior not known for other insectivores, but long known as a characteristic of shrews. Thus, Komarek (1932) in describing the hunting of *Sorex cinereus*, notes, "During most of the time he was under observation, about ten minutes, he kept up a twittering of short, high-pitched squeaks, only stopping long enough to get a grub or other insect."

It may be said further that in those features in which *Solenodon* differs from *Nesophontes*, it is by no means true that *Solenodon* is always the more tenrecoid and *Nesophontes* the more shrew-like. As noted above, in anterior dentition *Nesophontes* is quite similar to some tenrecids, particularly to such a genus as *Orizoryctes*.

The large hypocones of *Solenodon* are decidedly more shrew-like than is the narrow cingulum seen in *Nesophontes*; the latter is more as in *Microgale*. Because of this development of the hypocone, the permanent P^4 of *Solenodon* is more like that of the Soricidae than is that of *Nesophontes*.

While the capitular facets on the dentary condyle of *Solenodon* are arranged as in the

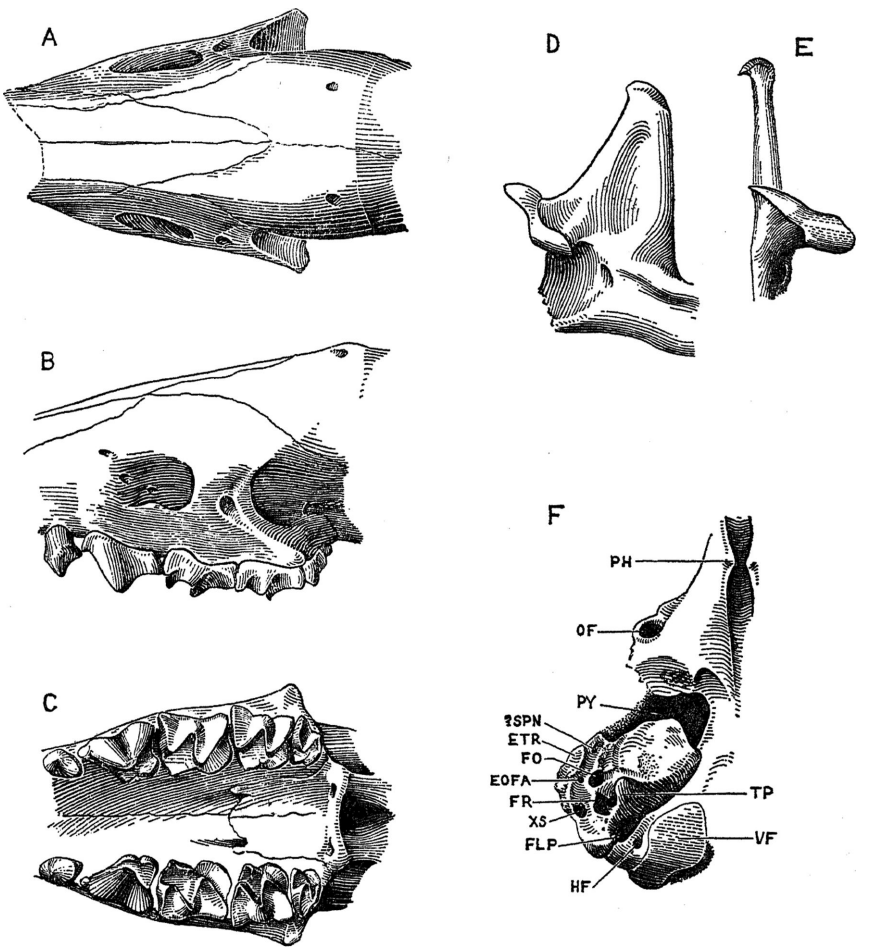

FIG. 30. The Chadronian soricid *Domnina*. A, B, C. Facial region of *D. ?gradata* (U.S.N.M. No. 12841). D. Mesial view of the posterior part of the dentary of *D. thompsoni*. E. Posterior view of the condyle of *D. thompsoni*. E. Posterior view of the condyle of *D. thompsoni*. F. *D. ?gradata*, auditory region. Abbreviations on page 129.

Oligocene shrew *Domnina*, the facets in *Nesophontes* are anomalous in being arrayed one ventroposterior to the other, rather than in a transverse row.

In spite of close resemblances between the Soricidae and the Antillean insectivores, it seems most improbable that either group is derived from the other. The most primitive known soricids are probably the Oligocene North American *Domnina* and the Miocene European *Heterosorex* (see Patterson and McGrew, 1937, and Simpson, 1941, for the former, and Gaillard, 1916, for the latter). These genera differ from other shrews and resemble the Antillean genera (as well as other mammals) in having a normal insertion of the temporal muscle on a simple scar on the mesial surface of the coronoid process. All other Soricidae show a unique specialization: the temporalis tunnels through the substance of the dentary to form a pocket continuous internally with the dentary canal (or, in *Diplomesodon*, separated from the canal by only a thin lamina of bone). This feature alone would appear to rule out all shrews save *Domnina* and *Heterosorex* from possible ancestry to the West Indian genera. Yet even *Domnina* and *Heterosorex* already show dental specializations that remove them from any phyletic line leading towards the West

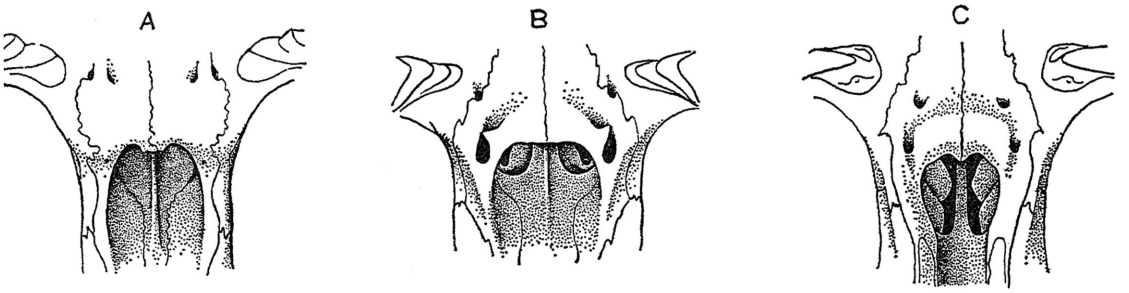

FIG. 31. Choanal regions of representative Tenrecidae (not to same scale), showing absence of well-defined postpalatine torus and the backward extension of the maxilla along the side of the pterygoid lamina. A. *Potamogale velox*. B. *Limnogale mergulus*. C. *Tenrec ecaudatus*.

Indian genera. Thus the buccal styles of the upper molars are already reduced and fail to form a raised outer border for the molar crown, while the teeth anterior to P_4 already have suffered reduction. Whether or not this reduction in the anterior teeth was in number as well as in size, it is impossible to say definitely, for in the shrew with the least-reduced dentition (*Domnina thomsoni* Simpson, 1941) the teeth anterior to P^4 are known only from their alveoli, which are six in number, the first being greatly enlarged. Because it cannot be proved that one or more of these teeth were not two-rooted, the number of these teeth may have been fewer than six (thus fewer than the number seen in *Solenodon* and *Nesophontes*); at any rate, there are at least two fewer dental roots anterior to P_4 in *Domnina thompsoni* than in the Antillean insectivores.

In addition, there is a probable cranial specialization common to *Domnina* and modern shrews (to go by U.S.N.M. No. 12841, a skull of *Domnina ?gradata*). There is no scar for the levator labii superioris proprius anterior to the orbit, and the muscle appears already to have moved up onto the frontal surface of the skull, as in the modern Soricidae.

On the other hand, the Soricidae cannot be derived from the Antillean genera. The large and funnel-shaped lacrimal foramen appears to be a specialization developed within the *Solenodon-Nesophontes* group, not seen elsewhere in the Lipotyphla. *Domnina* (*fide* U.S.N.M. No. 12841) shows essentially the same type of lacrimal foramen seen in modern soricids, a small hole on the side of the face between the infraorbital foramen and the orbital rim, this hole opening into a duct that curves upward and forward over the infraorbital foramen. In *Solenodon* and *Nesophontes* the very large foramen is on the orbital rim, and the duct follows a straight course dorsal to the infraorbital foramen. However, *Domnina* shows a weak vertical crest on the side of the face just anterior to the lacrimal foramen. This crest, not seen in modern shrews, may be the homologue of the orbital rim of *Solenodon* and *Nesophontes*.

The more primitive shrews have a strong, hook-like metacromion of the scapula, as in most insectivores (*Potamogale* excepted). The West Indian genera appear to be specialized in the great reduction and lobe-like form of

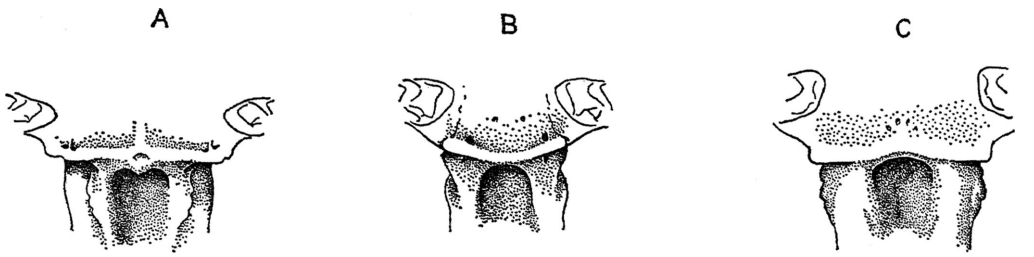

FIG. 32. Choanal region of representative Soricidae, to show the postpalatine torus (not to the same scale). A. *Myosorex caffer*. B. *Sorex palustris*. C. *Blarina brevicauda*.

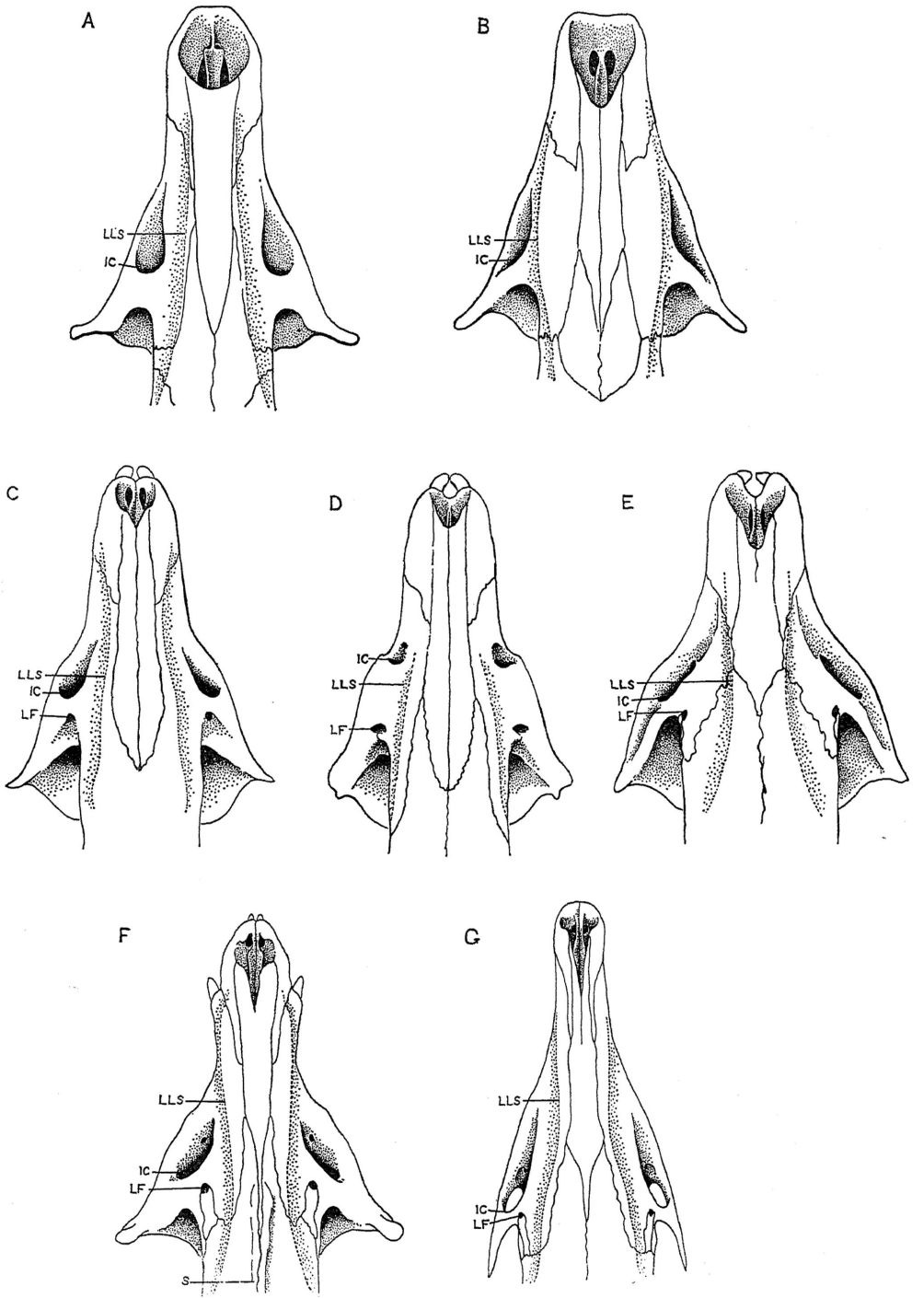

FIG. 33. Dorsal view of the facial portion of the skull in representative Tenrecidae (not to same scale). A. *Potamogale velox*. B. *Limnogale mergulus*. C. *Nesogale* sp. D. *Geogale aurita* (juvenile). E. *Echinops telfairi*. F. *Tenrec ecaudatus*. G. *Hemicentetes semispinosus*. Abbreviations on page 129.

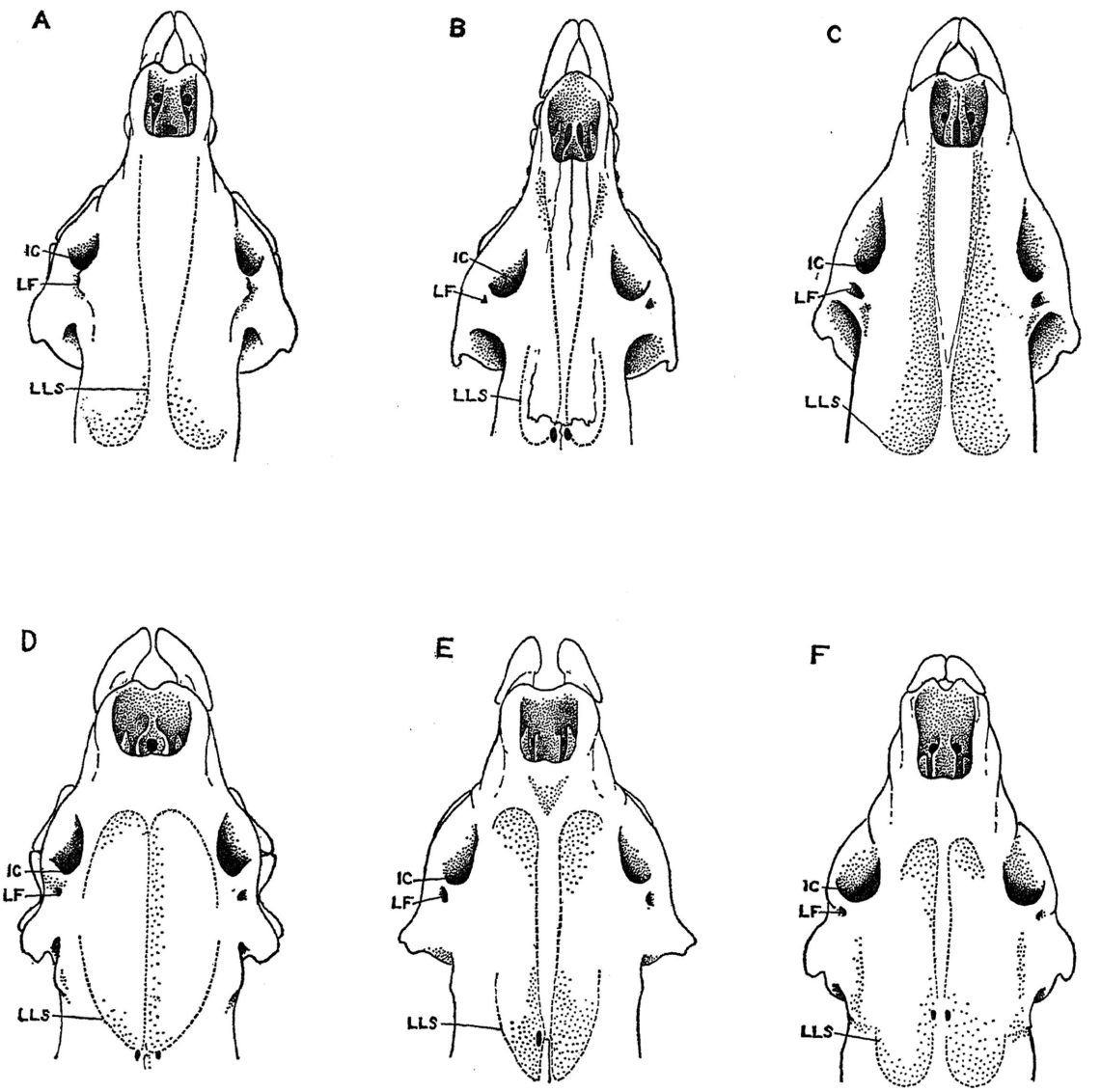

FIG. 34. Dorsal view of facial portion of skull in representative Soricidae (not to same scale). A. *Myosorex caffer*. B. *Sorex palustris*. C. *Diplomesodon pulchellum*. D. *Anourosorex squamipes*. E. *Blarina brevicauda*. F. *Chimarrogale leander*. Abbreviations on page 129.

the metacromion. The great enlargement of the foramen magnum in *Solenodon* and *Nesophontes* would also appear to be a specialization away from soricid conditions.

In the dentition the trend in molar-style development among the Antillean forms appears to have been almost the exact opposite of that seen in shrews, for, rather than obliteration of the stylar wall, there has been a hypertrophy.

The separation between the Soricidae and the Antillean genera must have taken place before the early Oligocene, for the Chadron *Domnina thompsoni* appears to be already specialized along soricid-like, rather than *Solenodon*- or *Nesophontes*-like, lines.

The Soricidae together with the Antillean genera appear to form a natural unit within the Lipotyphla, most strikingly characterized by the absence of the basisphenoid bulla, but also held together by many details of cranial structure, and, so far as can be deter-

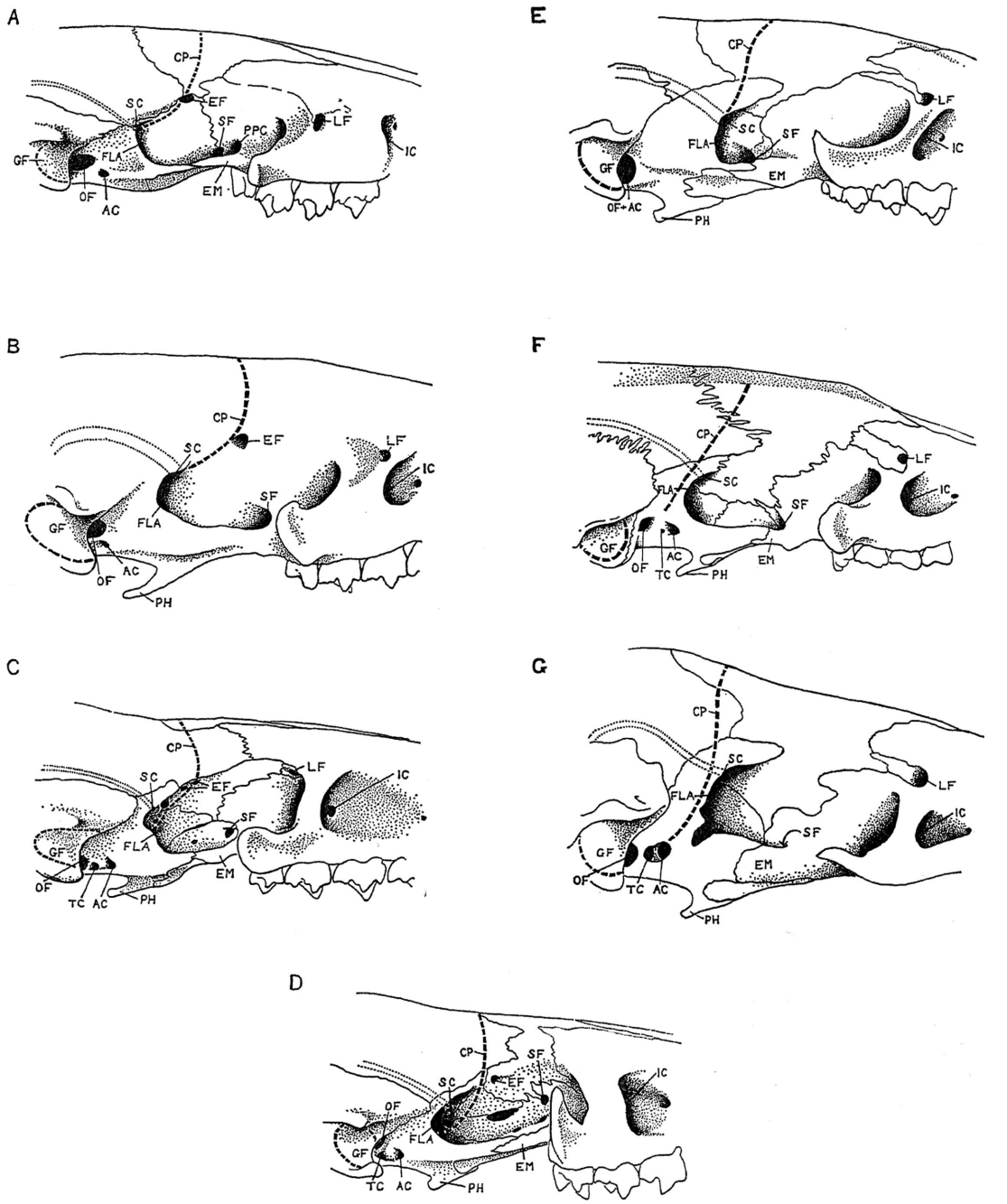

FIG. 35. Orbital region of skull in representative Tenrecidae (not to same scale). A. *Geogale aurita* (juvenile). B. *Nesogale* sp. C. *Limnogale mergulus*. D. *Potamogale velox*. E. *Echinops telfairi* (exceptional specimen with confluent foramen ovale and alisphenoid canal). F. *Tenrec ecaudatus*. G. *Hemicentetes semispinosus*. Abbreviations on page 129.

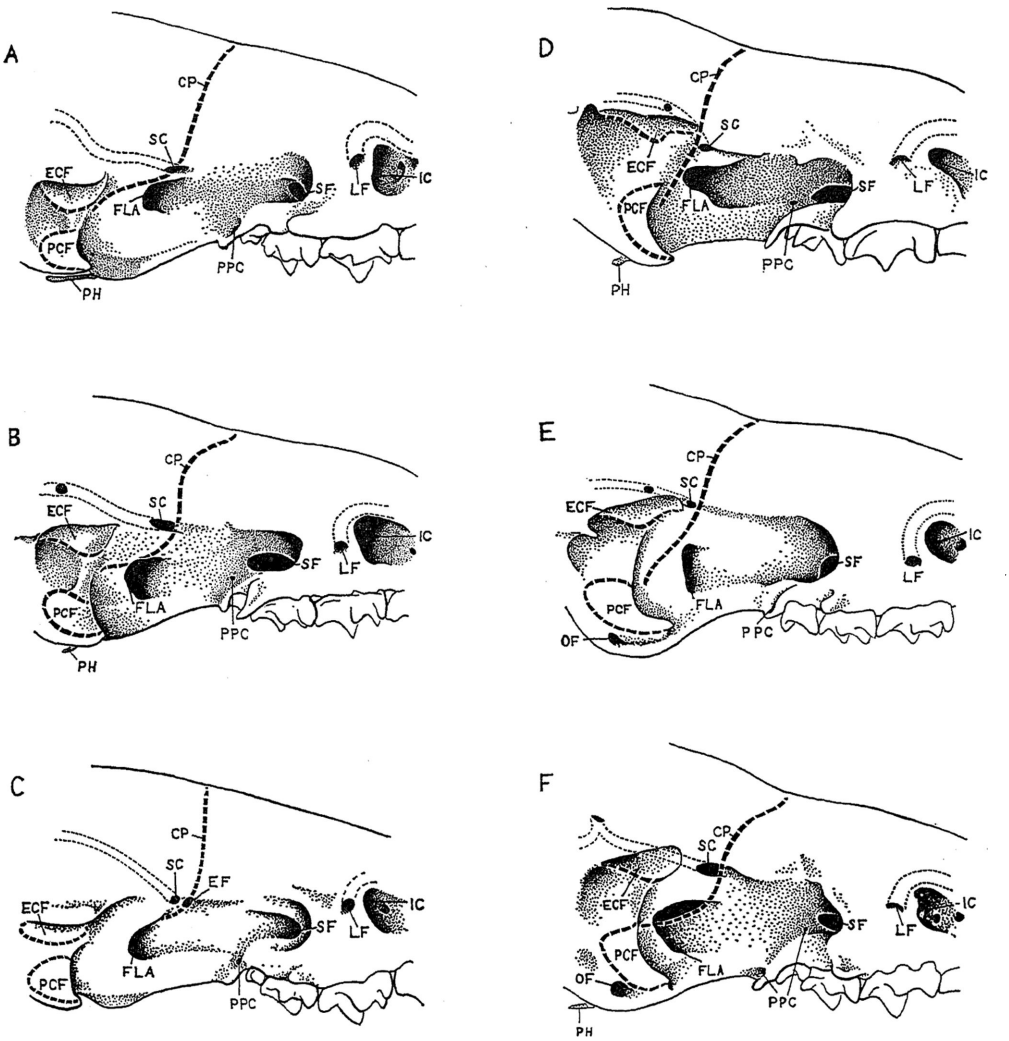

FIG. 36. Orbital region of skull in representative Soricidae (not to same scale). A. *Myosorex caffer*. B. *Sorex palustris*. C. *Diplomesodon pulchellum*. D. *Anourosorex squamipes*. E. *Blarina brevicauda*. F. *Chimarrogale leander*. Abbreviations on page 129.

mined from living forms, the great development of lateral glands and the structure of the fetal membranes.

Within this group, the West Indian genera appear to be more closely related to one another than to the shrews and might reasonably be included in the same family, for which the older name is Solenodontidae. These two families, Soricidae and Solenodontidae, might most conveniently be grouped in a superfamily Soricoidea of the Lipotyphla.

It seems likely to me that the closest relatives of the Soricoidea (as here defined) are not the Talpidae, but rather the Tenrecidae (including Potamogalidae) and their probable relatives, the Chrysochloridae. Some discussion of this is pertinent to the question of the affinities of the Solenodontidae, because Winge regarded *Nesophontes* as a primitive talpid, and Dobson was struck by the similarities of *Solenodon* to the talpid *Desmana*.

The talpids have been associated with the soricids primarily on the basis of the dilambdodont molar pattern, a pattern that has been developed independently by a variety of mammals (e.g., bats, tupaiines, didelphids,

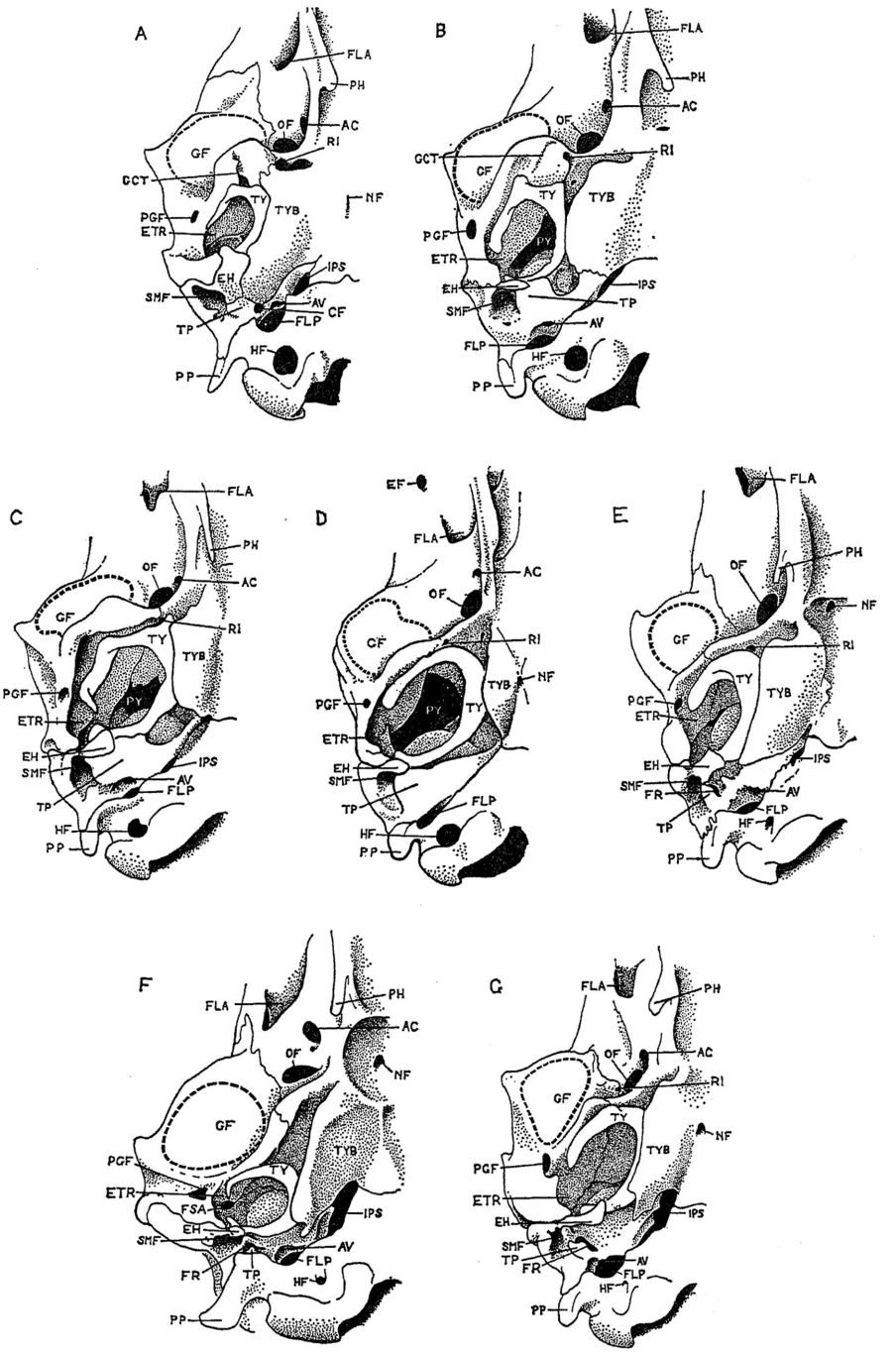

FIG. 37. Tympanic region of skull, with auditory ossicles removed, of representative Tenrecidae (not to same scale). A. *Potamogale velox*. B. *Limnogale mergulus*. C. *Nesogale* sp. D. *Geogale aurita*. E. *Echinops telfairi* (exceptional specimen with confluent foramen ovale and alisphenoid canal). F. *Tenrec ecaudatus*. G. *Hemicentetes semispinosus*. Abbreviations on page 129.

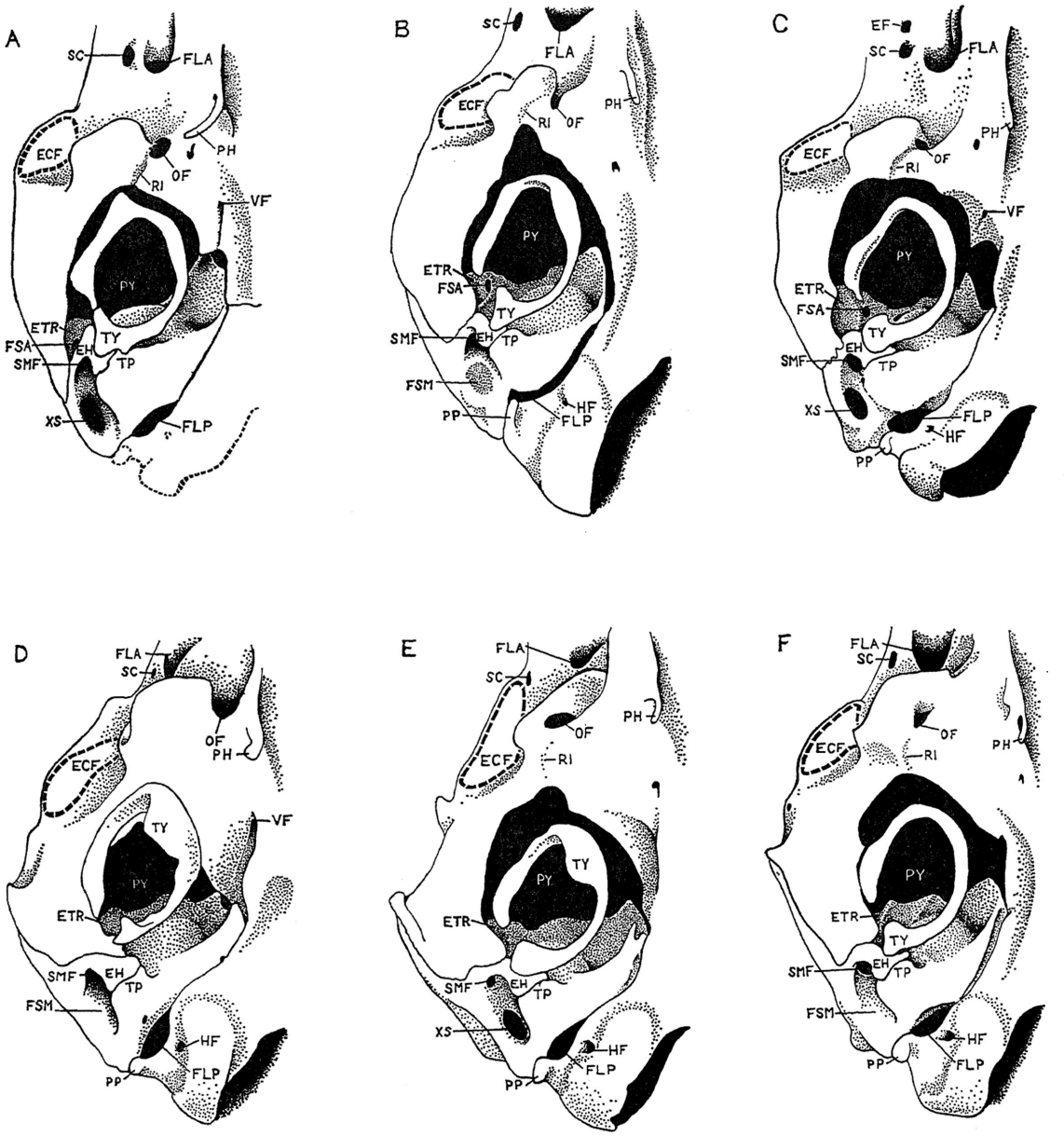

FIG. 38. Tympanic region of the skull, auditory ossicles removed, of representative Soricidae (not to same scale). A. *Myosorex caffer* (occipital missing in figured specimen). B. *Sorex palustris*. C. *Diplomesodon pulchellum*. D. *Anourosorex squamipes*. E. *Blarina brevicauda*. F. *Chimarrogale leander*. Abbreviations on page 129.

and primitive pantodonts). In cranial structure, however, the talpids appear to be much more closely allied to the erinaceids. The supposedly shrew-like general appearance of such talpids as *Uropsilus* can as easily be interpreted as a resemblance to such forms as *Hylomys* and *Neotetracus* among the erinaceids.

In the following cranial features the talpids appear to be closer to the erinaceids than to the Soricoidea, while the tenrecids agree with the soricoids in these same features:

1. Presence of a complete zygomatic arch, formed from a zygomatic process of the maxilla, a small jugal, and a zygomatic process of the squamosal. If the Dimylidae, for which

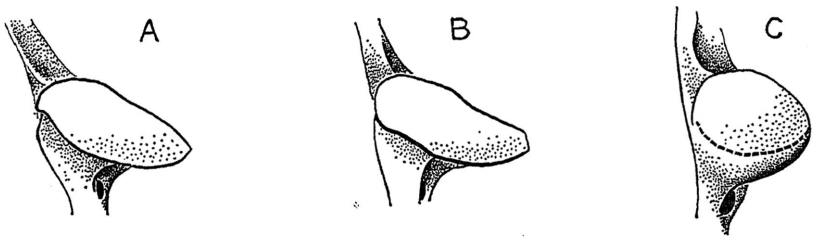

FIG. 39. Posterior view of left dentary condyle in representative Tenrecidae (not to same scale). A. *Potamogale velox*. B. *Limnogale mergulus*. C. *Tenrec ecaudatus*.

no information is available, be ignored, the Talpidae and Erinaceidae appear to be alone among the Lipotyphla in retaining a complete primary zygomatic arch. The Chrysochloridae have a complete arch, but this appears to be a secondary structure, derived by hypertrophy of a free zygomatic process of the maxilla such as seen in *Tenrec*. Roux (1947) has found a separate ossification center in the zygomatic process of the chrysochlorids, but this does not contradict the homology with the zygomatic process of the maxilla of tenrecids, for Roux also found a separate ossification center in the zygomatic process of the maxilla of *Setifer*, and Leimgruber (1939) found a similar ossification center in *Tenrec*. The shape of the zygomatic process is the same in tenrecs and chrysochlorids: strap-like, with a posterior expansion, so that the structure somewhat resembles the outlines of a lacrosse bat. That the arch in chrysochlorids is secondary is suggested by the absence of any trace of a zygomatic process of the squamosal. While Roux believes the zygomatic ossification center represents a jugal bone in chrysochlorids and tenrecs, it should be borne in mind that at no stage is there a separate formed bone set off by sutures, and that in the newly born skull of *Amblysomus hottentotus* studied by Broom (1916) the zygomatic process was quite continuous with the maxilla, although other cranial sutures were quite conspicuous. Additional ossification centers within the maxilla are common among mammals, without implication of bone fusions. Thus, in man, a mammal with a perfectly distinct and normal jugal bone, there is an additional ossification center of the maxilla (malar center) corresponding in position to the zygomatic center of chrysochlorids and tenrecs (Terry, *in* Schaeffer, 1942, p. 162). At any rate, the jugal of chrysochlorids, tenrecids, soricids, and solenodontids never has the independence seen in the young of talpids and erinaceids, and, in the present author's opinion, is probably totally absent.

The statement sometimes made that *Heterosorex* of the Soricidae possesses a zygomatic arch is not borne out by Gaillard's

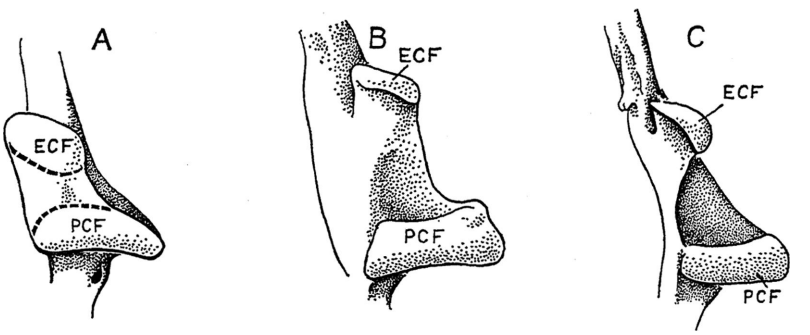

FIG. 40. Posterior view of left dentary condyle(s) in representative Soricidae (not to same scale). A. *Diplomesodon pulchellum*. B. *Blarina brevicauda*. C. *Anourosorex squamipes*. Abbreviations on page 129.

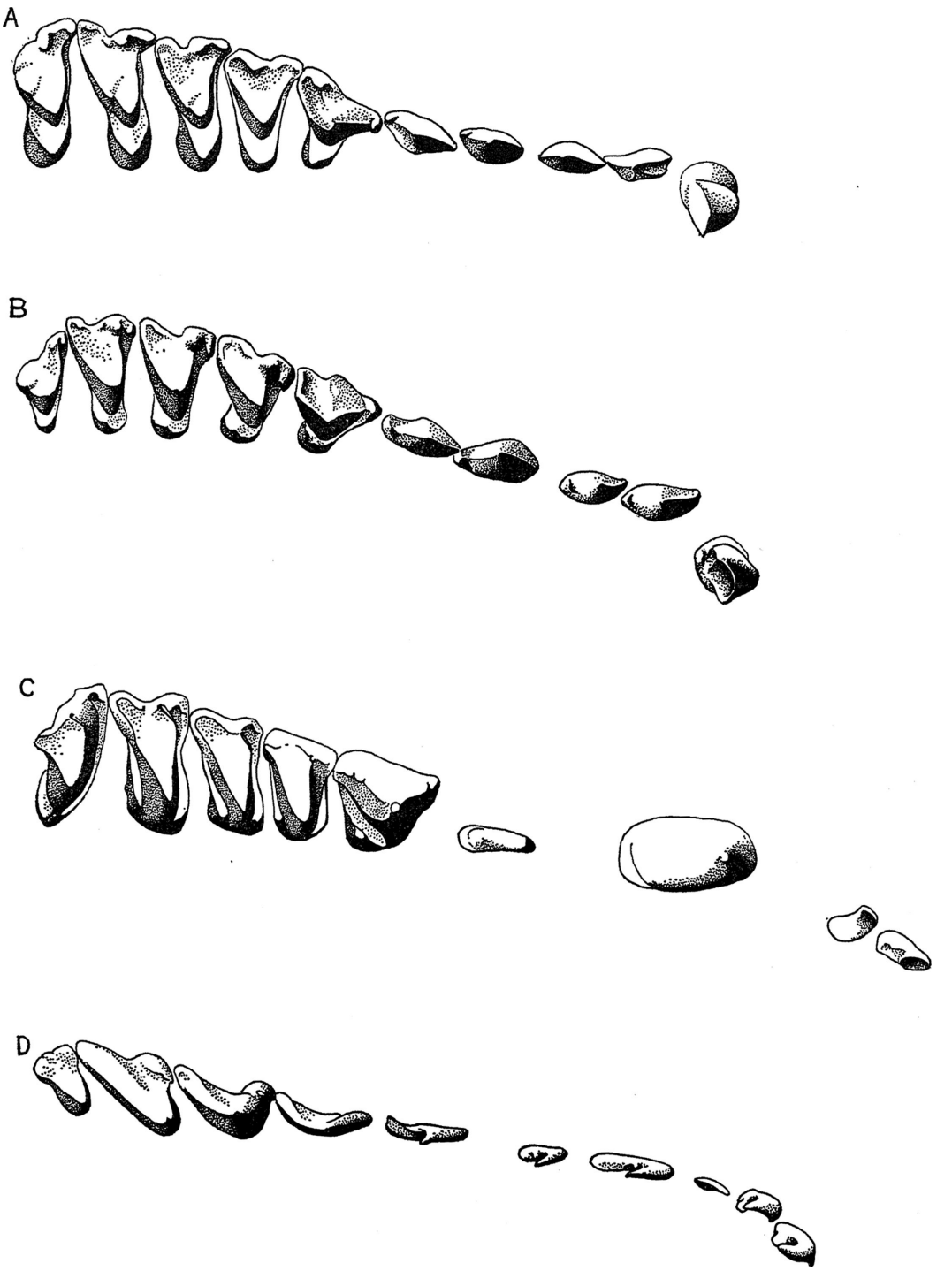

FIG. 41. Occlusal view of upper dentition in representative Tenrecidae (not to same scale). A. *Potamogale velox*. B. *Limnogale mergulus*. C. *Tenrec ecaudatus*. D. *Hemicentetes semispinosus*.

(1916) original description and figures. *Heterosorex* shows much better developed maxillary and squamosal zygomatic processes than do most shrews, but the arch is incomplete in the middle, and there is no indication of a jugal. Similarly, the statement that *Desmana* lacks the arch appears to be based on broken skulls.

It may be fitting to cite here the statement of Grassé (1955, p. 1642), with which the present author is in full agreement: *La tendance à la reduction de l'arc zygomatic aboutit*

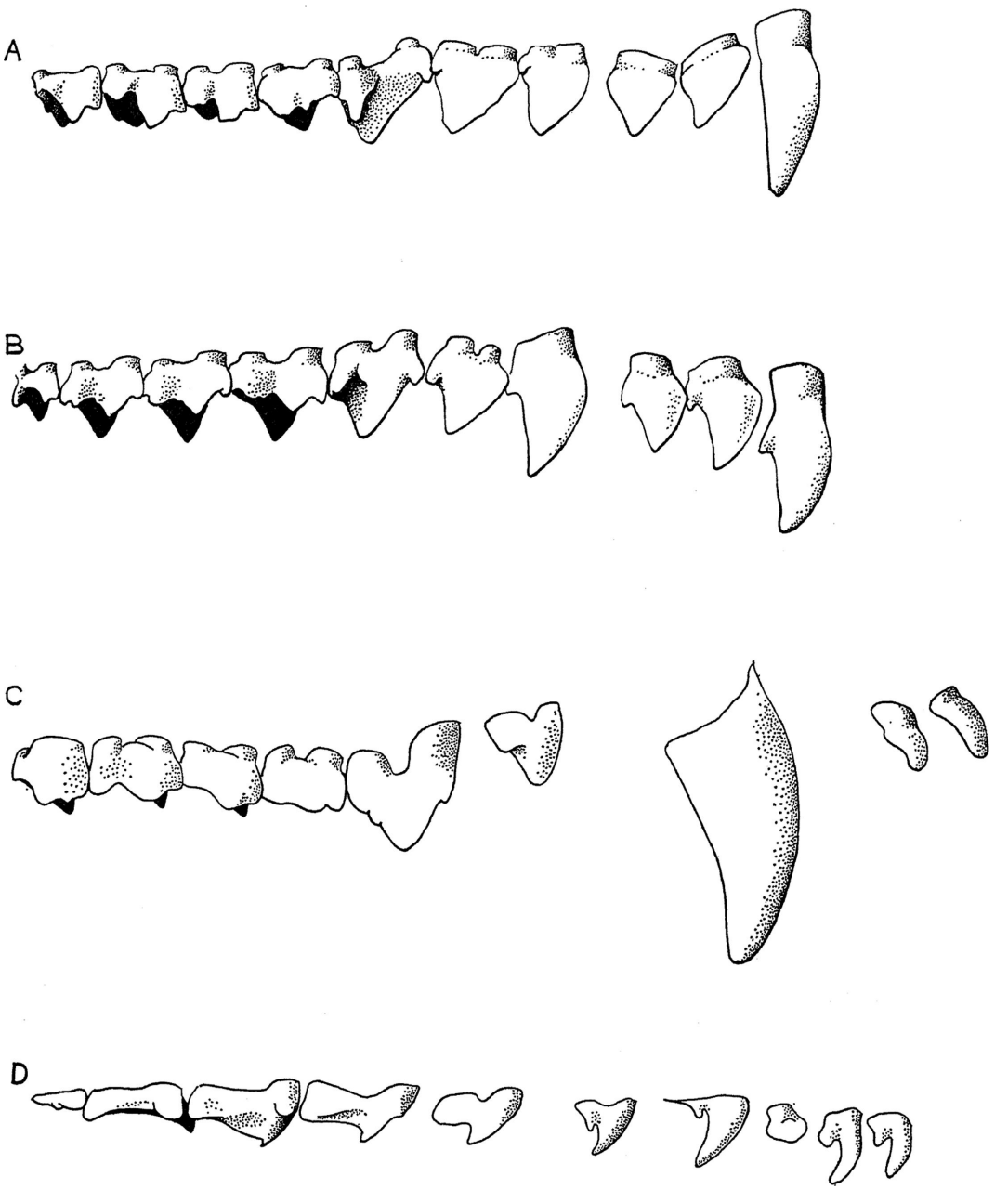

FIG. 42. Buccal view of upper dentition of representative Tenrecidae (not to same scale). A. *Potamogale velox*. B. *Limnogale mergulus*. C. *Tenrec ecaudatus*. D. *Hemicentetes semispinosus*.

chez les Soricidae à la disparition totale du dit arc. Si on attribue à ce fait une valour phylogénétique, et nous pensons qu'il doit en être ainsi, on découvre que la fusion des Talpidae et des Soricidae en une même superfamille (Soricoidea) a quelque chose d'artificiel. Le moins que l'on puisse dire, c'est qu'il s'agit de deux lignées évolutives distinctes depuis des temps extrêmement reculés."

the laminae appear to be present but to have lost their laminate form and to have become inflated into vesicles (so far as can be determined from dried skulls, by great dilation of the pterygoid canal). This is quite unlike the condition in the soricoids and tenrecs, in which this portion of the skull is concave, rather than inflated. Intermediate conditions between the laminate and the vesicular ecto-

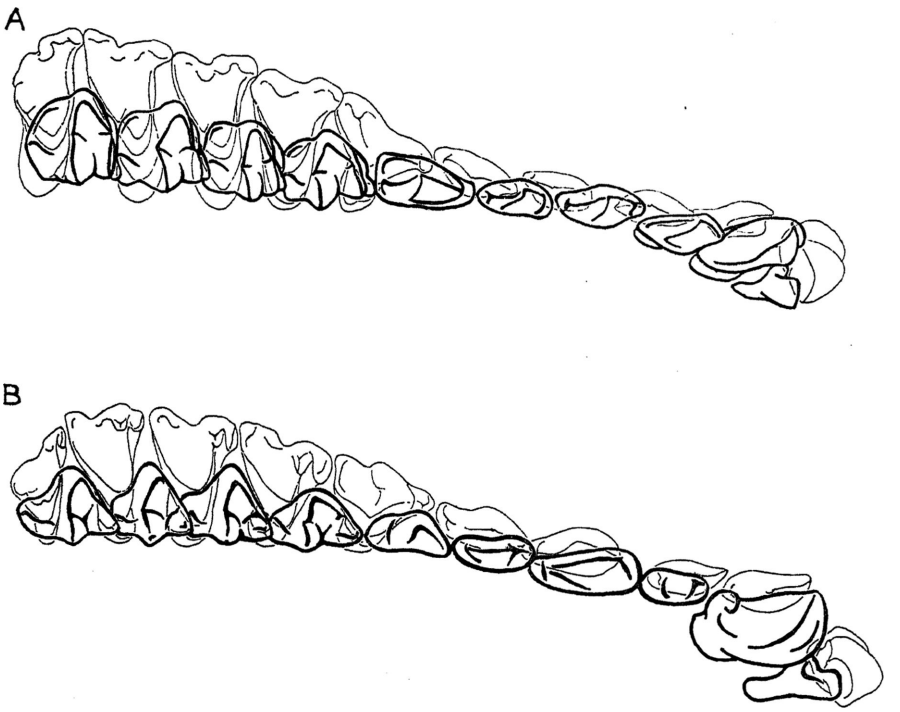

FIG. 43. Occlusion diagrams (not to same scale). A. *Potamogale velox*. B. *Limnogale mergulus*.

It may be said in partial confirmation of this that the Oligocene *Domnina* shows the same degree of reduction of the zygoma seen in living shrews.

2. Presence of ectopterygoid laminae, formed by the alisphenoid and dividing the pterygoid fossa into dorsolateral and ventromedial moieties. This is as in the Erinaceidae, whereas these laminae are absent in the Soricidae, Solenodontidae, Tenrecidae, and Chrysochloridae. This feature is clear cut in primitive talpids (e.g., *Uropsilus*, *Desmana*) but is disguised in advanced moles (e.g., *Talpa*, *Scalopus*), in which these laminae are often said to be absent (as by True, 1897). Actually, pterygoid process are seen in such a genus as *Parascalops*.

3. Absence of any sort of squamosal postglenoid process. In the Soricidae, Solenodontidae, Tenrecidae, and Chrysochloridae the entoglenoid process has been converted into a postglenoid process, a modification so peculiar as to suggest real relationship. In moles the jaw articulation is braced posteriorly by the ear and the jaw articulation is essentially as in the Erinaceidae, although relatively higher on the skull.

In addition to these features that separate the Talpidae and the Erinaceidae on the one hand from the Soricoidea plus the Tenrecidae

and the Chrysochloridae on the other, it may be mentioned that moles show a very different type of basicranial specialization from that seen in shrews, *Nesophontes*, and *Solenodon*. Rather than the widely open tympanic cavity seen in the Soricoidea, the moles have developed the tympanic wing of the basisphenoid into a large bulla, frequently subdivided into air cells and fitting tightly against the tympanic; the talpid epitympanic recess is large, rather than reduced; and the pyriform fenestra is absent, although the bone is very thin and fragile in *Uropsilus*.

Moreover, while cranial structure makes it impossible to derive moles from shrews, even the most primitive of moles show specializations, presumably for fossorial life, that remove them from possible ancestry to any other group of the Lipotyphla. Thus, even *Uropsilus* shows the peculiar talpid feature of articulation of the clavicle with the greater tuberosity of the humerus. Kistin (1929) concluded, "since all the Talpidae, from the extremely fossorial *Scalopus* to the shrew-like *Uropsilus* which does not use its limbs for digging, agree in the humero-clavicular joint, it is quite certain that the group has descended from a common ancestor that already had acquired this joint." *Amphidozotherium* from the Quercy Phosphorites shows the unique features of the mole humerus fully developed. While Schlaikjer (1933) referred

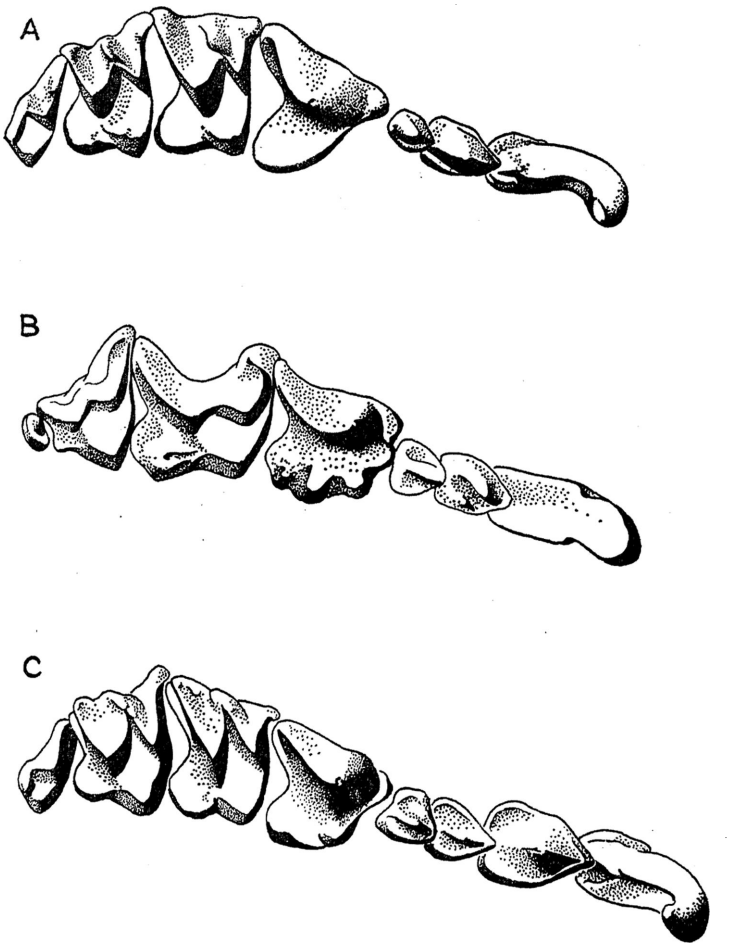

FIG. 44. Occlusal view of upper dentition in representative Soricidae (not to same scale). A. *Diplomesodon pulchellum*. B. *Anourosorex squamipes*. C. *Myosorex caffer*.

to the Talpidae a humerus (*Arctoryctes* Matthew) lacking any of the features of the proximal end characteristic of moles (e.g., facet for clavicle, tunnel-like biceps groove, styloid deltoid process, and dorsally displaced caput), this bone was not found in association with any recognizable mole remains, and cludes that the Talpidae diverged from an essentially erinaceid-like stem quite early, primarily as a fossorially modified line, and that the tenrecids and soricoids had a common ancestry specialized from a primitive erinaceid condition in three main features: (1) modification of the entoglenoid process into

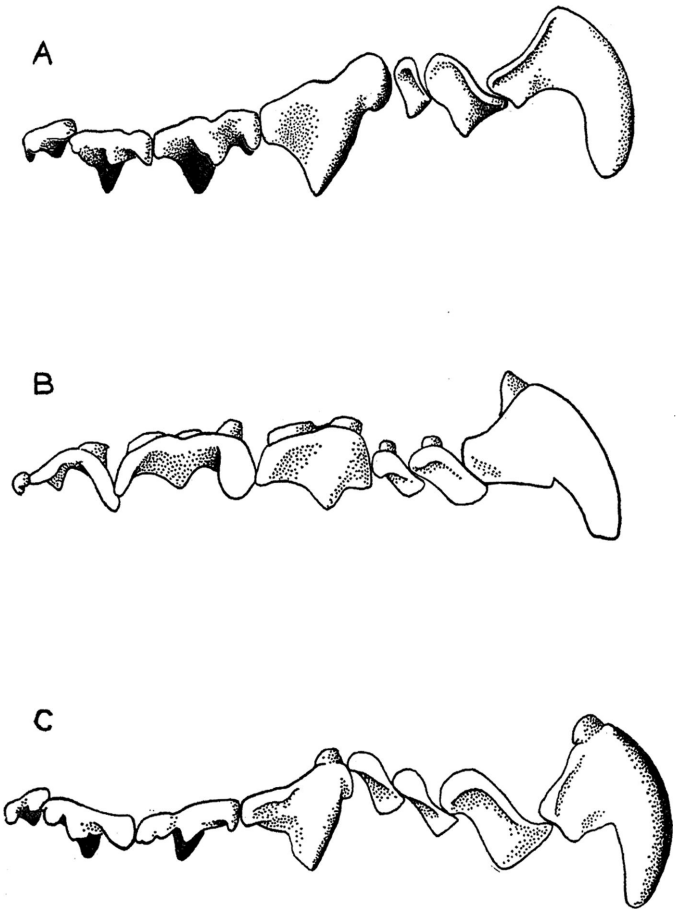

FIG. 45. Buccal view of upper dentition in representative Soricidae (not to same scale). A. *Diplomesodon pulchellum*. B. *Anourosorex squamipes*. C. *Myosorex caffer*.

Schlaikjer's allocation was probably erroneous, particularly as Galbreath (1953) has reported humeri from the Cedar Creek Oligocene which do show the characteristic talpid biceps channel.

Uropsilus also shows a typically talpid occiput; that is, a dome-like inion with the supraoccipital extending far forward on the roof of the skull between the parietals.

From these points the present author con- a postglenoid process; (2) loss of jugal and interruption of the jugal arch; and (3) loss of ectopterygoid laminae.

These three features perhaps form a functional association. The modified jaw articulation provides a ginglymous articulation (secondarily modified in *Tenrec*, *Hemicentetes*, *Setifer*, and *Echinops* by the narrowing of the dentary condyle to allow slight rotation of each dentary around a longitudinal axis pass-

TABLE 2

SKULLS OF TENRECIDAE, *Solenodon*, *Nesophontes*, AND *Soricidae* COMPARED

	Tenrecidae	*Solenodon*	*Nesophontes*	Soricidae
Rostrum	Moderate or long	Long	Long	Shortened
Narial border of nasals	V-shaped notch or concave	Transverse	Transverse or concave	Transverse or convex
Origin of levator labii superioris proprius	Temporal fossa	Side of rostrum	Side of rostrum	Top of frontal
Origin of erector vibrissorum	Zygomatic process of maxilla	Zygomatic process of maxilla	Zygomatic process of maxilla	Zygomatic process of squamosal
Nuchal crest when strong	Vertical	Horizontal	Horizontal	Horizontal
Vascular foramina in dorsal surface of frontal	Absent	Absent or poorly developed	Absent	Usually present
Lacrimal foramen	Small or absent	Large, funnel-like	Large, funnel-like	Small
Lacrimal duct	Straight	Straight	Straight	Curving upward and forward
Postpalatine torus	Not defined	Strong, with lateral corners	Strong, with lateral corners	Strong, with lateral corners
Maxilla produced along pterygoid crest, causing dorsal orifice of palatine canal to join sphenopalatine foramen	Yes	No	No (sutures not clear; based on foramina)	No
Pterygoid hamular process	Strong, hook-like (except in *Geogale*)	Minute or absent	Minute or absent	Minute or absent
Optic foramen	Confluent with foramen lacerum anterius or concealed by alisphenoid	Exposed	Just concealed by alisphenoid	Confluent with foramen lacerum anterius or concealed by alisphenoid
Suboptic foramen	Absent	Present	Absent	Absent
Sinus canal foramen	In foramen lacerum anterius	Distinct	Distinct	Distinct
Alisphenoid canal	Present	Present	Present	Absent
Transverse canal	Present or absent	Present	Present	Absent
Capitular facets in glenoid fossa	One	Two	Two (?, cartilages unknown)	Two

TABLE 2—(*Continued*)

	Tenrecidae	*Solenodon*	*Nesophontes*	Soricidae
Capitular facets on dentary	One	One, partly divided	One, partly divided	One, partly divided (*Domnina*), or two
Deep pocket for temporalis on mesial side of coronoid process	No	No	No	Yes (except in *Domnina* and *Heterosorex*)
Bullar (tympanic) wing of basisphenoid	Well developed, meets tympanic	Vestigial, not meeting tympanic	Vestigial, not meeting tympanic	Absent (possible vestige in *Soriculus* and *Anourosorex*)
Exit from ear of ramus inferior of stapedial artery	By foramen or sharply defined notch	By open groove	By open groove	By open groove
Pyriform fenestra	Absent or rudimentary, not reducing alisphenoid or squamosal contribution to tympanic roof	Large, nearly excluding alisphenoid and squamosal from tympanic roof	Large, nearly excluding alisphenoid and squamosal from tympanic roof	Large, nearly excluding alisphenoid, and quite excluding squamosal, from tympanic roof
Epitympanic recess	Moderately large to large, mainly in squamosal	Much reduced, mainly in petrosal	Much reduced, mainly in petrosal	Much reduced, mainly in petrosal
Ramus superior of stapedial artery enters cranial cavity by	Own foramen between petrosal and squamosal	Pyriform fenestra	Pyriform fenestra	Usually by own foramen in petrosal
Tympanohyal	Ventral to posterior limb of tympanic, may (*Potamogale*) underlap latter considerably	Dorsal to tympanic, not reaching latter or promontorium	Dorsal to tympanic, not reaching latter or promontorium	Dorsal to tympanic, reaching promontorium to aid or replace latter in support of tympanic
Groove for auricular nerve	Open	Bridged by bone	Open	Open
Tympanic process of petrosal	Weak to strong	Strong	Strong	Weak to moderately strong
Exposure of inferior petrosal sinus	Constricted from foramen lacerum posterius	Continuous with foramen lacerum posterius	Continuous with foramen lacerum posterius	Continuous with foramen lacerum posterius
Postglenoid foramen	Present, small	Present, large	Present, small	Absent
Paroccipital (jugular) process	Projecting	Vestigial	Projecting	Projecting (e.g., *Suncus*) or vestigial (e.g., *Blarina*)

TABLE 2—(*Continued*)

	Tenrecidae	*Solenodon*	*Nesophontes*	Soricidae
Foramen magnum	Small to moderately large	Very large	Very large	Small to moderate
Condyloid canal	Absent (except in Potamogalinae)	Present	Present	Absent
Upper molars	"Zalambdodont" (one main cusp)	"Zalambdodont" (one main cusp)	"Dilambdodont" (three main cusps)	"Dilambdodont" (three main cusps)
Buccal stylar wall of upper molars	Present	Present	Present	Absent (except for mesostyle)
Posterior portion of buccal stylar wall of upper molars	Reduced	Enlarged as curved secant crest	Enlarged as curved secant crest	Absent (an isolated cuspule in *Myosorex*)
First complex upper premolar	P^3 (P^4 in *Geogale*)	P^4	P^4	P^4
Buccal roots of M^1	Two	Two	Two	Usually three
Hypocone	Absent, unless represented by "protocone"	Moderately large	Narrow cingulum	Enormous, basin-like
Milk teeth	Kept until fully adult	Shed early	Shed early	Uncalcified, not piercing gum
Canines	Projecting and grooved or smooth, or premolariform	Premolariform, smooth, inconspicuously enlarged	Conspicuously projecting, grooved, semipremolariform	Completely premolariform or absent (homologies uncertain)
Upper incisors	Equal, or first enlarged, proclivous	First greatly enlarged, opisthoclivous	First moderately enlarged, slightly proclivous	First greatly enlarged, proclivous, peculiar in form
Lower incisors	Subequal or I_2 enlarged, bilobate or not	I_2 enlarged, none bilobate	Subequal, bilobate (I_1 unknown)	One (homology uncertain); much enlarged, often polycuspidate, never bilobate
Largest lower incisor	Smooth or obscurely grooved	Conspicuously channeled	Bilobate, grooved, but not channeled	Obscurely to distinctly grooved, not channeled
P_4	Molariform	Molariform	Not molariform	Not molariform
Talonids	Reduced	Reduced, except on M_3	Not reduced	Not reduced, or reduced on M_3

ing from the mandibular symphyseal region along each dentary to the glenoid articulation). Associated with this ginglymous articulation, the pterygoid muscles change their function from ectental movement of the jaw to raising of the jaw, assisting the temporalis and masseter. The masseter thus loses some of its importance as a levator of the jaw, permitting reduction of the zygomatic arch.

The Tenrecidae and Chrysochloridae have retained many primitive lipotyphlan features lost in the Soricoidea, such as simple glenoid capitular facet, basisphenoid bulla, foramen for the inferior ramus of stapedial artery, and unreduced tympanic wing of the alisphenoid. Perhaps the long retention of the milk teeth, nearly or quite until full size is reached, is also a primitive feature; it is, at any rate, in strong contrast to soricoids, in which the milk teeth are either lost very early (*Solenodon* and *Nesophontes*) or are not even calcified (Soricidae). On the other hand, the tenrecids and chrysochlorids have developed specializations of their own: zalambdodonty, apparently independent of that seen in *Solenodon*, and different in detail (the small cusp seen in *Solenodon* and here interpreted as the paracone is not seen in tenrecids and chrysochlorids); reduction of the posterior portion of the buccal stylar wall of the upper molars while retaining the anterior portion of the wall in strong development; forward shift of the change in upper cheek-tooth complexity from before P^4 to before P^3; reduction of the postpalatine torus; development of the tympanic wing of the epihyal; and loss of the conus inguinalis. In addition, there is a shortness of the cartilaginous proboscis in this group that is probably secondary, to judge from erinaceids and talpids. It is in strong contrast to the condition in shrews and *Solenodon* (*Nesophontes* unknown), in which the free cartilaginous proboscis is subequal to the length of the preorbital portion of the bony skull; in the Old World zalambdodonts the free proboscis is conspicuously shorter than the bony muzzle.

The tenrecids and chrysochlorids appear to form a natural assemblage which might be grouped as a superfamily Tenrecoidea. While the Chrysochloridae are strikingly modified, their relationships appear to lie with tenrecs, and grouping them with the Tenrecidae appears to express this best. There is no evidence of this group outside Africa and Madagascar, and it may be supposed that the group had an African origin. The genus *Tenrec* and its immediate allies have become amazingly similar to *Erinaceus*, not only in development of spines and reduction of the tail, but in some cranial features, such as development of a basisphenoid pit. To the present writer's eye, this parallelism has been more thoroughgoing than the merely dental parallelism between *Solenodon* and the tenrecoids.

A CLASSIFICATION OF THE LIPOTYPHLA

THE PRECEDING REMARKS on relationships among Lipotyphla may be formalized in the following classification:

ORDER LIPOTYPHLA

HAECKEL, 1866 (as suborder).

Orbital wing of palatine greatly reduced, barely entering orbit, far separated from the lacrimal by maxillo-frontal contact (in *Potamogale* the great vertical depth of the choanal passage causes the vertical lamina of the palatine to be much enlarged and superficially like an orbital wing; however, it is not pressed against the ethmoid and lies lateral to the choanal passage); ethmoid exposed within orbit dorsal to palatine (but this exposure may become fused with orbital wing of frontal); lacrimal without facial wing or lacrimal tubercle; nasals undilated posteriorly, retracted from narial border anteriorly; jugal reduced or absent, separated from lacrimal; entotympanic absent; tympanic only slightly, if at all, produced mesial to attachment of tympanic membrane; true postglenoid process absent, but replaced functionally in some by the entoglenoid process of the squamosal; no venous foramen lacerum medium, but postglenoid foramen usually present; foramen ovale distinct, surrounded by alisphenoid; alisphenoid canal usually joined with fossa for Gasserian ganglion; posterior clinoid processes and bony dorsum sellae absent; subarcute (paraflocular) fossa very deep and sharply defined; paroccipital process distinct from mastoid process (vestigial in *Solenodon*); alisphenoid entering, at least slightly, into tympanic roof; fenestra rotunda opening into a pit bordered behind by a raised rim of the petromastoid.

Tympanic rami of internal carotid with characteristic and constant pattern, essentially similar to that of lemuroids and menotyphlans with the addition of a large ramus inferior of the stapedial artery; carotid entering tympanic cavity without giving off any branch to run mesial to ear cavity; carotid forked upon the promontorium into two branches, the arteria promontorii and arteria stapedia; arteria promontorii running diagonally across promontorium to enter cranial cavity by two branches, the main branch passing between petromastoid and basisphenoid to join circle of Willis, the other (Vidian branch) passing through pterygoid canal to pierce basisphenoid and emerge on interior of cranium lateral to hypophyseal fossa; arteria stapedia dividing into two branches after passing between crura of stapes, the ramus superior piercing petromastoid to enter cranial cavity as the middle meningeal artery, while the inferior ramus leaves the ear by notching, piercing, or grooving the preotic crest of the alisphenoid and joins the internal maxillary artery.

Pubes not in direct contact beneath visceral mass, the ischia broadly separated from each other; body of astragalus lying directly under tibia; neck of astragalus distinct, the head wide and flat-oval; trochlea of astragalus symmetrical, not extending onto plantar side of body.

Teeth always of a sharp-cusped carnivorous type, the crown covered completely by enamel; teeth all rooted, the roots presenting interradicular crests of Butler that fit in corresponding grooves between the alveoli; Pd^{4}_{4} never resembling a normal tribosphenic molar, contrasting with the molars except in forms with premolar-like modification of the molars; intestine without trace of caecum; stomach simple.

Testes never descending into a true scrotum, the abdominal muscle wall uninterrupted; ovary enclosed within a periovarian sac; uterus bicornuate; vagina simple, moderately long; no menstrual bleeding; urethra with prostatic bulb.

North America to (Recent) northern South America; Greater Antilles; Europe; Africa, Madagascar; Asia through the Sunda Islands to Celebesian region; Philippines; introduced (*Suncus murinus*) in New Guinea. Not known positively before late Eocene but certainly existent before that time.

SUBORDER ERINACEOMORPHA

SABAN, 1954 (including some fossil forms here excluded, and excluding Talpidae).

Zygomatic arch retained, formed by zygomatic processes of maxilla and squamosal

and by jugal bone; no postglenoid process of any kind; ectopterygoid laminae present, but sometimes (some Talpidae) converted into bulbous swellings; posterior lacerate foramen restricted by contact of a lobe of the basioccipital with the petromastoid ventral to the inferior petrosal sinus; recti abdominis crossed at pelvic insertion; basisphenoid bulla well developed, meeting tympanic.

Family ERINACEIDAE

Bonaparte, 1838.

Buccal styles of upper molars forming only a low cingulum; first two molars subequal in size; paracone not lambdoid, metacone lambdoid or not; temporalis not extending forward to level of front of orbit; levator labii superioris originating on frontal over orbit; tympanic narrow; occiput flat or concave; nuchal crest extended upward; supraoccipital not extending forward between parietals; clavicle not articulated with humerus; vagina persistent; clitoris not peniform.

Oligocene to Pliocene of North America; ?Eocene to Recent of Europe; ?Oligocene to Recent of Asia; Miocene to Recent of Africa; Recent of Philippines.

Family DIMYLIDAE

Schlosser, 1887.

For dental remains from the upper Oligocene and Miocene of Europe. Dentition similar to that of Erinaceidae, but P^4 and M^1 hypertrophied; M^1 with divided mesostyle, as in Talpidae; P^4 a simple large conical tooth (as in most Talpidae); border of bony naris as in Talpidae, with flaring tuberosities formed by ascending rami of premaxillae; P_4 and M_1 greatly enlarged.

Family TALPIDAE

Gray, 1825.

Upper molars with distinct buccal styles, including a doubled mesostyle, which form an outer wall to the teeth; first two molars subequal in size; paracone and metacone both lambdoid; temporalis extending forward nearly or quite to level of front of orbit; levator labii superioris originating from base of zygoma; tympanic broadened by enlargement of recessus meatus, forming a flask-shaped bulla in many genera; occiput greatly inflated into a dome-like convexity, with a pair of fenestrae dorsolateral to foramen magnum; nuchal crest, when well developed (*Desmana*), directed backward (as in Soricoidea); supraoccipital (?joined with interparietal) extended forward between parietals on roof of skull, greatly displacing nuchal line forward; clavicle articulated with humerus, joining a formed facet on the greater tuberosity; vagina completely occluded except in breeding season; clitoris peniform, bearing urethral termination; primarily fossorial forms.

Uppermost Eocene to Recent of Europe; upper Oligocene to Recent of North America; Recent of Asia.

Suborder SORICOMORPHA

Saban, 1954 (including Talpidae and some fossil groups here excluded).

Zygomatic arch interrupted by loss of jugal (secondarily reformed in Chrysochloridae by contact of zygomatic process of maxilla with squamosal); no ectopterygoid laminae (vestigial in some Tenrecidae, such as *Geogale*); entoglenoid process modified into a postglenoid process; except in Chrysochlorideae, posterior lacerate foramen extended forward as a slit between petromastoid and basioccipital, exposing the posterior portion in the inferior petrosal sinus.

Superfamily TENRECOIDEA

Simpson, 1931 (including also Palaeoryctidae, Apternodontidae, Solenodontidae).

Basisphenoid with well-developed tympanic wing, in contact with tympanic; epitympanic recess large to very large; squamosal making extensive contribution to roof of tympanic cavity; pyriform fenestra absent or incipient, the alisphenoid forming a large portion of the tympanic roof and providing a large bony area of origin for the tensor tympani; tympanohyal ventral in plane to the posterior limb of the tympanic; sinus canal foramen opening within the foramen lacerum anterius; inferior ramus of stapedial artery passing out of ear through a foramen in the alisphenoid, or a foramen that is converted into a sharply incised notch; glenoid capitular facet simple; nuchal crest, when produced (e.g., *Tenrec*, *Potamogale*), extended upward;

maxilla produced backward along the lateral border of lamina defining the interpterygoid (choanal) fossa; no postpalatine torus; hamular process well developed (except in *Geogale*); levator labii superioris proprius arising within temporal fossa and partially covered by the temporalis; well-developed anal glands, but no lateral glands; allantoic sac large to very large; male reproductive tract without conus abdominalis.

Milk dentition well developed, persisting nearly or quite until the animal reaches full size; premolars gradually becoming more complex from front to back of series.

Africa and Madagascar.

Family TENRECIDAE

Gray, 1821.
(Potamogalidae Allman, 1869).

Orbitosphenoids well developed, meeting on the midline of the floor of the braincase to form a presphenoid intervening between mesethmoid and basisphenoid (as in most mammals and all insectivores except chrysochlorids); zygomatic process of maxilla falling far short of squamosal, leaving a conspicuous gap in zygoma; condyloid (venous) canal absent, except in Potamogalinae; tympanic narrow and ring-like; occiput essentially flat (somewhat dome-like in *Geogale*); nuchal line not forwardly displaced (except in *Geogale*); digits, except hallux and pollex, with three phalanges.

Recent of tropical West Africa; Pleistocene to Recent of Madagascar. Miocene of Kenya (Butler and Hopwood, 1957).

Family CHRYSOCHLORIDAE

Mivart, 1868 (1867–1868).

Orbitosphenoids greatly reduced or absent, not forming a presphenoid, nor separating mesethmoid from basisphenoid; zygomatic process of maxilla hypertrophied to reach squamosal or squamosal and parietal, forming a (secondary) zygoma; venous condyloid canal present, opening at lateral border of foramen magnum just dorsal to occipital condyle; tympanic forming a flask-shaped bulla through enlargement of recessus meatus and development of ossified meatal tube; occiput developed into an inflated hemispherical dome (cf. Talpidae); nuchal line displaced far forward on roof of skull; phalangeal formula of manus, 2-2-1-1 or 2-2-1-2; of pes, 2-2-2-2-2.

Miocene to Recent of Africa, mainly in the southern half, but one species extending to the Cameroons.

Superfamily SORICOIDEA

Gill, 1872 (including Talpidae, excluding Solenodontidae).

Tympanic wing of basisphenoid represented at most by a crest lying mesial to Eustachian cartilage and falling far short of tympanic; epitympanic recess much reduced in size; squamosal virtually excluded from roof of tympanic cavity by pyriform fenestra, the latter greatly developed and almost excluding alisphenoid from tympanic roof, so that the tensor tympani arises mostly from the membrane of the pyriform fenestra; posterior limb of tympanic entirely ventral to tympanohyal; sinus canal foramen opening outside the foramen lacerum anterius; inferior ramus of stapedial artery leaving ear by a relatively shallow groove in the alisphenoid; two glenoid capitular facets; nuchal crest, when produced, produced backward; maxilla not extending backward along wall of interptergoid fossa; postpalatine torus distinct; pterygoid hamuli reduced or absent; levator labii superioris not arising from temporal fossa, nor overlapped by temporalis; anal glands vestigial or absent, but lateral glands well developed; allantoic sac much reduced; conus abdominalis present.

Milk dentition reduced or (Soricidae) totally uncalcified, soon lost before attainment of full size; P^4 abruptly more complex than the preceding premolars.

Geographic range equivalent to that of order.

Family SOLENODONTIDAE

Dobson, 1882.
(Nesophontidae Anthony, 1916).

Milk dentition calcified, functional; upper molars with strongly developed buccal stylar wall, forming a cutting crest divided into anterior and posterior portions by a narrow fissure, the posterior portion curved linguad onto the occlusal surface anteriorly; hypocone moderate (*Solenodon*) or a narrow cingulum (*Nesophontes*), not filling the interdental embrasure; lacrimal foramen very

large, like a trumpet bell in form, on orbital margin, leading into a straight lacrimal duct; tympanohyal small, separated from tympanic and promontorium; alisphenoid and transverse canals present; postglenoid foramen present; levator labii superioris proprius arising from maxilla dorsal to lacrimal foramen; venous condyloid canal present; foramen magnum very large, extending well above dorsal extremity of occipital condyle; metacromion a triangular, flap-like projection of the scapular spine.

Cuba, Isle of Pines, Hispaniola, Ile de la Gonave, and Puerto Rico (Recent and sub-Recent).

Family SORICIDAE

Gray, 1821.

Milk dentition uncalcified, non-functional; buccal stylar wall of upper molars absent; hypocones very large, filling the interdental embrasures; lacrimal foramen a small puncture anterior to the orbital margin, immediately behind anterior orifice of infraorbital canal, leading into a canal that curves upward and forward dorsal to infraorbital canal; tympanohyal large, in contact with tympanic and promontorium; alisphenoid and transverse canals absent; levator labii superioris arising from frontal dorsal to orbit near midline (this point usually marked out by a paired foramen); venous condyloid canal absent; postglenoid foramen absent; foramen magnum of only moderate size, barely exceeding occipital condyle in dorsal extent; metacromion hook-like.

Lowermost Oligocene to Recent of continental North America; Recent of northern South America; Oligocene to Recent of Europe; Miocene to Recent of Africa; Pliocene to Recent of Asia; Recent of Madagascar, Philippines, and Celebes and Moluccas. (*Suncus coeruleus*, a commensal of man introduced into New Guinea.)

Families Excluded from the Lipotyphla

Leptictidae: This family, frequently associated with the Erinaceidae, appears to be closely related to the Tupaiidae, and should be placed with that family, either in the Primates, or, as I prefer, in the Order Menotyphla. The auditory bulla is formed by a large, crescentic entotympanic largely enclosing a simple, ring-like tympanic that lacks a recessus meatus; it is thus similar to that of the Tupaiidae. Other features indicating relationship to the Tupaiidae, rather than to the Lipotyphla, are: lacrimal with facial wing; jugal large, with lacrimal contact; palatine with large orbital wing that meets lacrimal; squamosal with true processus postglenoideus; no bony channel for a ramus inferior of the stapedial artery; alisphenoid canal separated by bone from the Gasserian fossa; strong dorsum sellae with clinoid processes; a strong pubic symphysis involving both pubis and ischium; trochlea of astragalus curving over proximal surface of body of astragalus.

Zalambdalestidae: Apparantly related to the Leptictidae, and with a similar triangular facial wing of the lacrimal, a large jugal in contact with the lacrimal, a true postglenoid process, and forwardly produced nasals. These features would rule out close relationship to the Lipotyphla.

Macroscelididae: This family makes some approach to the Lipotyphla in the absence of a postglenoid process, presence of a fossa above the auditory meatus like that in Erinaceidae, well-developed recessus meatus in the tympanic, absence of dorsum sellae, foramen in the Folian process for the chorda tympani (at least in *Rhynchocyon*), and presence of an elongated flexible nasal proboscis. However, other features, such as the pubic symphysis that involves the ischia, astragalar trochlea extending over the proximal end of the astragalar body, large jugal in contact with lacrimal, large facial wing of lacrimal, entotympanic auditory bulla, paroccipital process formed jointly by mastoid and exoccipital (rather than by exoccipital alone), and large intestinal caecum, all suggest that it is to the Tupaiidae and Leptictidae that the Macroscelididae are most closely related.

Palaeoryctidae (including Deltatheridiidae): The basicranial features of *Palaeoryctes* that set this genus apart from the Lipotyphla are outlined in a section above (see pp. 176–180). *Deltatheridium* shows expanded posterior ends of the nasals in contact with facial expansions of the lacrimals, quite unlike any lipotyphlan. Again unlike Lipotyphla, there appear to be a quite distinct

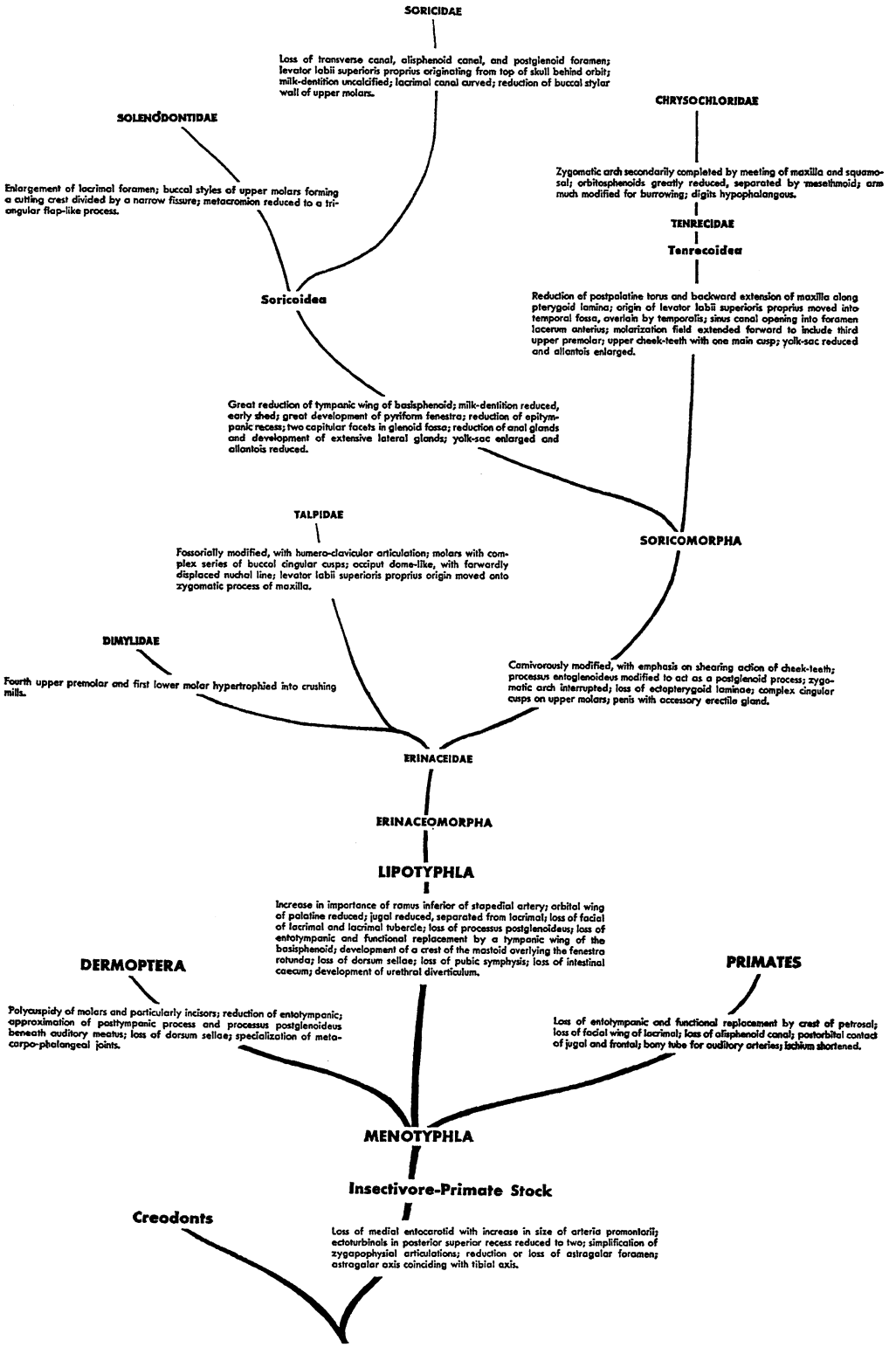

FIG. 46. Suggested sequence of some major anatomical innovations in the Lipotyphla.

postfrontal process and lacrimal tubercle. The poor preservation of *Didelphodus* skulls prevents detailed observation, but the general resemblance to *Deltatheridium* and the presence of a lacrimal tubercle rule against lipotyphlan affinities.

APTERNODONTIDAE: The reasons for regarding this family as non-lipotyphlan are outlined in a preceding section (pp. 164–174).

NYCTITHERIIDAE: As this group is essentially a form family for poorly known fossil forms showing general, but not definitive, resemblance to the Soricidae or Talpidae, the family cannot with any assurance be referred to the Lipotyphla, although future discoveries may indicate that some of its members are lipotyphlan. The group must be regarded as a convenient "pigeonhole" for forms *incertae sedis*.

PANTOLESTIDAE: This family has a true postglenoid process and a strong frontoparietal constriction. In addition, *Bessoecetor*, at least, has Pd_4 completely molariform. This is not true of the Lipotyphla, except in the irrelevant case of Tenrecidae and Chrysochloridae in which it appears to be a matter of premolariform molars, rather than molariform deciduous premolars. This is, however, a resemblance to the Menotyphla, as well as other mammals. Although relationship to the Apatemyidae has not been suggested for the pantolestids, the two families share a unique feature: a pit on the lateral surface of the dentary, beneath M_1 or M_2, into which pit open two mental foramina, one anterior and the other posterior; when inadequately prepared, this pit for two foramina may appear a single, simple, mental foramen.

MIXODECTIDAE: This aberrant and insufficiently known family has been included in the Insectivora only because it does not fit well elsewhere, and shows no considerable resemblance to any lipotyphlan family. The astragalus has the trochlear surface extended over the proximal end of the astragalar body onto the volar surface, a menotyphlan (leptictid) and rodentian feature, but the family cannot be said to show definite resemblance to any other mammalian group.

APHELISCIDAE: This poorly known family shows no resemblance to the Lipotyphla, having a zygoma that is compressed, even though weak, with greater vertical than transverse diameter; a true postglenoid process; a long infraorbital canal, with its anterior orifice over P^3; and a strong frontoparietal constriction. The teeth are peculiar, particularly P_4^4, but are reconcilable with those of *Mixodectes*. The family is *incertae sedis*.

CONCLUSIONS

IT HAS BEEN THE NECESSITY in paleontology to classify most mammals, and particularly such small forms as insectivores, on the basis of dentition, for ordinarily it is only fragments of dentition that endure from distant times as a "fossil record." Where a very complete series of intermediate dental forms from the intermediate time levels exists, inferences on the relationship of the organisms based on the similarities and differences in tooth structure have usually met objective standards of reliability. That is:

1. The structure of other organs, where known, follows the same evolutionary trends postulated on the basis of the teeth alone.

2. Far more often than might be expected from random chance, predictions of the nature of structures unknown at the time have been confirmed when these structures were later investigated.

3. Forms thought to be closely related on the basis of dental morphology also show grouped distribution in time and space, rather than being scattered at random.

4. Where the evolutionary lines postulated on the basis of the teeth extend into the Recent, detailed anatomical and physiological investigation of the supposed living representatives shows approximately the same degree of likeness and unlikeness that would be expected from the phylogeny based on teeth.

As an example of a phylogeny based largely on dentition that has passed objective tests, we might cite the phylogeny of the Perissodactyla. The very full dental record of fossil perissodactyls has allowed the framing of an evolutionary hypothesis that may be tested against an unusually large number of fossil skeletons and against the comparative anatomy of Recent representatives of three of the five main lines of perissodactyl evolution. In every case the hypothesis based on teeth has led to predictions that accord fully with the facts, and this hypothesis must be regarded as much "proved" as any hypothesis can be in an inductive science.

But it is another matter when considerable gaps occur in the record, for, while it is true that mammals with "nearly identical" dentitions are usually "very closely related," it cannot be said that mammals with "rather similar" teeth are "rather closely related." In the pages above I have noted the remarkable similarity in molar form between a primitive multituberculate (*Ctenacodon*) and a specialized pteropodid bat (*Harpionycteris*). Other examples are numerous; one need but turn to Ameghino's numerous incorrect, but dentally justifiable, allocations of endemic South American groups to Holartic mammalian orders.

Nor are dental features always uniform within otherwise homogeneous groups. Thus, among the Chiroptera, the family Phyllostomatidae shows a range in dental variation essentially equal to that of the entire order, for while some (Phyllostomatinae, Chilonycterinae) have normal dilambdodont teeth like those of the Vespertilionidae, Emballonuridae, and Rhinolophidae, others (particularly the Phyllonycterinae) show close resemblance to the Pteropodidae in degeneration of the cusp relief and rostro-caudal elongation of the molars; while among the Stenoderminae occur molar modifications without parallel.

It must be recalled that, while study of the numerous intermediate fossil dentitions demonstrates the naturalness of the Perissodactyla, a study of the dentition of the living horses, tapirs, and rhinoceroses would not easily lead to this conclusion. For while the basicranium, foot structure, myology, and visceral anatomy of living perissodactyls show great similarities, the teeth are an exception to this, and no obvious ordinally diagnostic similarity exists among the dentitions of the three living families.

From this it seems reasonable to conclude that in the case of the "zalambdodonts" the study of teeth is on uncertain ground, for the time gaps between supposed fossil zalambdodonts are great (lower Palaeocene, Oligocene, Miocene, and Pleistocene).

Further, the "zalambdodont" tooth is not so easily defined even in dental terms as some literature might suggest. Several quite different patterns of buccal styles are embraced in the "zalambdodont" category of molars. To

my mind, it is most questionable, in the absence of good fossil time series, to ignore the stylar wall and to assume that it has been the sculpture of the lingual portion of the molar crown that has been most conservative.

The "zalambdocone" of the *Solenodon* molar does not bite along the same line as does the paracone of the premolars; for while the premolar paracone bites lateral to the lower dentition, the molar "zalambdocones" bite between the trigonids of the lower molars, above the small talonids. The "zalambdocone" of the molars of *Solenodon* is even more markedly lingual relative to the paracone of Pd^4, a tooth of the same dental series as the molars, and instead occludes in the same relative position as the protocone of Pd^4. The "zalambdocone" of *Solenodon* appears to be the protocone (as held by Gregory, 1910) and the diminutive "protocone" to be the lingual cingulum. (However, G. M. Allen's argument that the zalambdocone of *Solenodon* is a metacone is not refuted by this point, as the metacone of *Nesophontes* bites lingual to the paracone.)

Such homologies of the cusps in *Solenodon* make the molars of that genus quite comparable with those of *Nesophontes*, the other West Indian genus of insectivores. *Nesophontes* and *Solenodon* show detailed similarity in the buccal styles of the molars and share a unique combination of cranial features.

By my interpretation of the molars of *Solenodon*, these teeth differ from those of *Nesophontes* primarily in the reduction of the sculptured relief of the upper molar trigons and lower molar talonids, with a corresponding emphasis on the simple shear between the upper molar trigon as a whole and the lower molar trigonid. This would appear an adaptation to increased longevity, for while the paracone and metacone are worn away in shrews in slightly over a year, *Solenodon* would appear to outlive this time by many years (Mohr, 1951, gives the maximum recorded life span in captivity for *Solenodon cubanus* as five years and seven months, and for *S. paradoxus* as seven years).

Whether or not the "zalambdocone" of the Tenrecidae is also the protocone is a difficult question, but in any case it seems likely that the zalambdodonty of the Tenrecidae is a development independent of the zalambdodonty of *Solenodon*. The latter genus shares numerous cranial specializations with the dilambdodont Soricoidea and particularly with the dilambdodont *Nesophontes*. Because the shrews and *Nesophontes*, as well as *Solenodon*, are much too specialized in these skull features to be ancestral to the tenrecids, it becomes impossible to draw up any phylogeny relating *Solenodon* especially to the tenrecids that does not call for altogether implausible coincidences in the cranial resemblance between *Solenodon* and the shrews and *Nesophontes*. In addition, the buccal styles of the tenrecid molar do not agree with those of *Solenodon* nearly so well as does the stylar wall of *Nesophontes*. In *Solenodon* and *Nesophontes* the anterior and posterior portions of the wall are separated by a narrow fissure, whereas in tenrecids the separation is a broad emargination, with the posterior portion much smaller and less secant than in the Antillean genera.

The fossil genus *Apternodus* (and its presumed relative *Oligoryctes*) show such extreme difference from *Solenodon* in skull structure that relationship to the Antillean genus appears impossible. Indeed, while *Solenodon* shows all the distinctive specializations of the Lipotyphla, *Apternodus* shows none of these features and does not even appear to be a member of the same order as the West Indian genus; the known anatomy of *Apternodus* is in better agreement with creodont affinities. The dental resemblance to *Solenodon* (or, for that matter, the Tenrecidae) appears far too lacking in detail to speak with much voice against the testimony of the skull.

Palaeoryctes, supposed to be ancestral to modern zalambdodonts, shows great dental difference from modern forms, particularly in the totally different stylar region and lingually elongate protocone. The supposed affinity to living zalambdodonts is not supported by the basicranium or by the structure of the axis. Rather, the basicranium and axis are of creodont type. The possibility of relationship to *Apternodus* deserves consideration, but the latter genus is so peculiarly specialized that no positive statement of its relationships is possible now. Certainly, the

known portions of *Palaeoryctes* show no convincing similarity to the corresponding regions of *Solenodon*, or any other living insectivore.

Solenodon and *Nesophontes* appear on osteological grounds to be more closely related to each other than to any continental form, and the buccal styles of the molars provide corroboration of this. It seems reasonable to believe that the evolution of the group took place in the West Indies. Probably the place of origin for this group was North America, for no insectivores have been recorded from South America, save the recent shrew *Cryptotis*, certainly not ancestral to the Solenodontidae. No insectivores have been found in the sediments of North America that could be regarded as ancestral to the West Indian forms; however, the Solenodontidae are a tropical group today, and probably are derived from a tropical ancestor. In the absence of known tropical American Tertiary insectivores, our ignorance of the ancestor of the Solenodontidae is not surprising.

The broader affinities of the West Indian insectivores appear definitely to be with the Soricidae. Indeed, if we were to draw up specifications for a hypothetical intermediate between *Solenodon* and the Soricidae, these specifications would differ only in one major respect from the known *Nesophontes*. This one feature, anterior dentition, in which *Nesophontes* fails to fall between *Solenodon* and the Soricidae, represents a resemblance of *Nesophontes* to the primitive Tenrecidae. As the tenrecoids probably had a common ancestry with the soricoids, this possibly represents retention in *Nesophontes* and primitive tenrecids of a feature of this common ancestor.

Above I note Ameghino's allocations of South American mammals to Holarctic groups. In most cases Ameghino was led to these judgments by dental evidence—evidence that appears quite convincing when examined in isolation. However, other workers (Roth, Scott, Sinclair, Simpson, and Patterson, to name but a few) with osteological material, and particularly cranial material, have shown conclusively that the Tertiary South American mammal fauna was a peculiar and highly endemic assemblage derived from a relatively very small number of Holarctic elements, but convergent in dentition to many different Holarctic groups.

The present author believes the Antillean fauna may represent an analogy to the Tertiary South American fauna in this regard, although on a much less grand scale, for it involves a much smaller number of forms and probably shorter times of isolation from the parent continental stocks for the various Antillean invaders.

SUMMARY

THE TWO GENERA of West Indian insectivores, *Solenodon* and *Nesophontes*, have been placed in separate superfamilies, Tenrecoidea and Soricoidea, respectively. This classification is based primarily on the sculpture of the lingual portion of the upper molars. Examination of the skull, however, reveals very close agreement between the two genera, and this agreement is seen further in the form of the buccal portion of the molars. So close is the apparent relationship between the two genera that they are here placed in the same family, Solenodontidae.

The fossil (Oligocene) genus *Apternodus* is not even a member of the same order (Lipotyphla) as its supposed relative *Solenodon*. *Apternodus* is so peculiarly specialized that its relationships are obscure, but its basicranial structure suggests creodont, rather than insectivore, affinities.

Palaeoryctes (Puerco), supposed to be an ancestral zalambdodont, is not related to any of the living zalambdodont groups, bearing only an equivocal dental resemblance to modern forms and showing a creodont-like rather than lipotyphlan-like basicranium. It is suggested that the families Deltatheridiidae and Palaeoryctidae be merged, under the latter name.

A classification of the lipotyphlous insectivores is presented, based primarily on cranial structure:

Order Lipotyphla
- Suborder Erinaceomorpha
  - Family Erinaceidae
  - Family Dimylidae
  - Family Talpidae
- Suborder Soricomorpha
  - Superfamily Tenrecoidea
    - Family Tenrecidae
    - Family Chrysochloridae
  - Superfamily Soricoidea
    - Family Solenodontidae
    - Family Soricidae

Solenodon and *Nesophontes* appear to represent a line that separated from a presoricid stem not later than the upper Eocene, and there is no reason to believe that the divergence of the two genera did not take place in the West Indies.

LITERATURE CITED

ÅRNBACK-CHRISTIE-LINDE, AUGUSTA
1912. On the development of the teeth of the Soricidae: an ontogenetical inquiry. Ann. Mag. Nat. Hist., ser. 8, vol. 9, pp. 601–625, figs. 1–9, pls. 18–19.

ALLEN, GLOVER MORRILL
1910. *Solenodon paradoxus*. Mem. Mus. Comp. Zoöl., vol. 40, no. 1, pp. 1–55, pls. 1–9.
1917. New fossil mammals from Cuba. Bull. Mus. Comp. Zoöl., vol. 61, pp. 1–12, pl. 1.
1918. Fossil mammals from Cuba. *Ibid.*, vol. 62, pp. 133–148, pl. 1.

ALLEN, JOEL ASAPH
1908. Notes on *Solenodon paradoxus* Brandt. Bull. Amer. Mus. Nat. Hist., vol. 24, pp. 505–517, 9 figs., pls. 28–33.

ALLMAN, GEORGE J.
1869. On the characters and affinities of *Potamogale*, a genus of insectivorous mammals. Trans. Zool. Soc. London, vol. 6, pt. 1, pp. 1–16, figs. 1–9, pls. 1–2.

AMADON, DEAN
1950. The Hawaiian honeycreepers (Aves, Drepaniidae). Bull. Amer. Mus. Nat. Hist., vol. 95, pp. 155–262, figs. 1–23, pls. 9–15, 15 tables.

ANTHONY, HAROLD ELMER
1916. Preliminary diagnosis of an apparently new family of insectivores. Bull. Amer. Mus. Nat. Hist., vol. 35, pp. 725–728, pl. 23.
1918. The indigenous land mammals of Porto Rico, living and extinct. Mem. Amer. Mus. Nat. Hist., new ser., vol. 2, pt. 2, pp. 331–435, figs. 1–55, pls. 55–75.
1919. Mammals collected in eastern Cuba in 1917. With descriptions of two new species. Bull. Amer. Mus. Nat. Hist., vol. 41, pp. 625–643, pls. 35–37.
1925. Mammals of Porto Rico, living and extinct—Chiroptera and Insectivora. Scientific Survey of Porto Rico and the Virgin Islands. New York, New York Acad-

emy of Sciences, vol. 9, pt. 1, pp. 1–96, figs. 1–28, pls. 1–15, 1 map.

BLAINVILLE, HENRI MARIE DUCROTAY DE

1840. Ostéographie des mammifères. Tome premier—Primatés-Secundatés. Livraison 6-H. Ostéographie des mammifères insectivores. Paris, J. B. Bailliere et fils, 115 pp.

BONAPARTE, CHARLES LUCIEN JULES LAURENT

1838. Synopsis vertebratorum systematis. Nuovi Ann. Sci. Nat., Bologna, vol. 2, anno 1, pp. 105–133.

BRANDT, JOHANNES FREDERICK

1833. De Solenodonte novo mammalium insectivororum genere. Mem. Acad. Imp. Sci. St. Petersbourg, ser. 6, vol. 2, pp. 459–478, pls. 1–2.

BROOM, ROBERT

1916. On the structure of the skull in *Chrysochloris*. Proc. Zool. Soc. London, pp. 449–459, figs. 1–3, pls. 1–2.

BUTLER, PERCY M.

1937. Studies of the mammalian dentition.—I. The teeth of *Centetes ecaudatus* and its allies. Proc. Zool. Soc. London, ser. B, vol. 107, pp. 103–132, figs. 1–28, pls. 1–3.

1939. The teeth of the Jurassic mammals. *Ibid.*, ser. B, vol. 109, pp. 329–356, figs. 1–12.

1948. On the evolution of the skull and teeth in the Erinaceidae, with special reference to fossil material in the British Museum. *Ibid.*, vol. 118, pp. 446–500, figs. 1–26.

1956. The skull of *Ictops* and the classification of the Insectivora. *Ibid.*, vol. 126, pp. 453–481, figs. 1–8.

BUTLER, PERCY M., AND A. TINDELL HOPWOOD

1957. Fossil mammals of Africa, No. 13. Insectivora and Chiroptera from the Miocene rocks of Kenya Colony. London, British Museum, iii+35 pp., 10 figs.

CABRERA, ANGEL

1925. Genera mammalium. Insectivora, Galeopithecia. Madrid, 232 pp., 18 pls.

COLBERT, EDWIN HARRIS

1942. An edentate from the Oligocene of Wyoming. Notulae Nat., no. 109, pp. 1–16, figs. 1–3, 1 pl.

DE BEER, GAVIN R.

1937. The development of the vertebrate skull. Oxford, Clarendon Press, xxiv+552 pp., 143 pls

DENISON, ROBERT HOWLAND

1938. The broad-skulled Pseudocreodi. Ann. New York Acad. Sci., vol. 37, pp. 163–256, figs. 1–32.

DOBSON, GEORGE EDWARD

1882–1890. A monograph of the Insectivora, systematic and anatomical. London, John Van Voorst, pt. 1 (1882), pp. 1–96; pt. 2 (1883), pp. 97–172, pls. 1–22; pt. 3 (1890), pls. 23–28. (This work was never completed.)

GAILLARD, CLAUDE

1916. Nouveau genre de musaraignes dans les dépôts miocènes de la Grive Saint-Alban (Isère). Ann. Soc. Linnéenne Lyon, new ser., vol. 62, pp. 83–98, figs. 1–8.

GALBREATH, EDWIN C.

1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. Paleont. Contrib. Univ. Kansas, Vertebrata, art. 4, pp. 1–120, figs. 1–26, pls. 1–2.

GILL, THEODORE

1872. Arrangement of the families of mammals with analytical tables. Smithsonian Misc. Coll., vol. 11, art. 1, pp. i–vi, 1–98.

GRASSÉ, PIERRE-PAUL (ED.)

1955. Traité de zoologie. Paris, Masson et Cie, vol. 17, fasc. 2, pp. 1173–2300, figs. 1095–2106, pls. 1–4.

GRAY, JOHN EDWARD

1821. On the natural arrangement of vertebrose animals. London Med. Reposit., vol. 15, pt. 1, pp. 296–310.

1825. Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. Ann. Phil., new ser., vol. 10 (vol. 26 of the whole series), pp. 337–344.

GREGORY, WILLIAM KING

1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., vol. 27, pp. 1–524, 32 figs.

1920a. On the structure and relations of *Notharctus*, an American Eocene primate. Mem. Amer. Mus. Nat. Hist., new ser., vol. 3, pt. 2, pp. 49–243, figs. 1–84, pls. 23–59.

1920b. Studies in comparative myology and osteology; no. IV. A review of the evolution of the lacrymal bone of vertebrates with special reference to that of mammals. Bull. Amer. Mus. Nat. Hist., vol. 42, pp. 95–263, figs. 1–196.

1949. The humerus from fish to man. Amer. Mus. Novitates, no. 1400, pp. 1–54, figs. 1–33.

HAECKEL, ERNST
1866. Generelle Morphologie der Organismen. Berlin, Georg Reimer, vol. 2, clx+462 pp., 8 pls.
HEIM DE BALZAC, H.
1954. Un genre inédit et inattendu de mammifère (insectivore Tenrecidae) d'Afrique occidentale. Compt. Rendus Acad. Sci., Paris, vol. 239, pp. 102–104, 1 fig.
HOUGH, MARGARET JEAN
1956. A new insectivore from the Oligocene of the Wind River Basin, Wyoming, with notes on the taxonomy of the Oligocene Tenrecoidea. Jour. Paleont., vol. 30, pp. 531–541, figs. 1–2, pl. 62.
KISTIN, ALBERT D.
1929. The mole clavicle. Jour. Mammal., vol. 10, pp. 305–315, figs. 1–5.
KOMAREK, E. V.
1932. Notes on mammals of Menominee Indian Reservation, Wisconsin. Jour. Mammal., vol. 13, pp. 203–209.
LACK, DAVID
1947. Darwin's finches. Cambridge, England, University Press, x+208 pp., 27 figs., 8 pls.
LECHE, WILHELM
1907. Zur Entwicklungsgeschichte des Zahnsystems der Saugethiere, zugleich ein Beitrag zur Stammesgeschichte dieses Thiergruppe. II. Theil. Phylogenie. 2. Heft. Die Familien der Centetidae, Solenodontidae und Chrysochloridae. Zoologica, Stuttgart, vol. 20, pt. 49, pp. 1–157, figs. 1–108, pls. 1–4.
LEIMGRUBER, CHARLES
1939. Le crâne primordial d'un embryon de *Centetes ecaudatus*. Biomorphosis, vol. 1, pp. 545–585, figs. 1–16.
MATTHEW, WILLIAM DILLER
1903. The fauna of the Titanotherium beds at Pipestone Springs, Montana. Bull. Amer. Mus. Nat. Hist., vol. 19, art. 6, pp. 197–226, figs. 1–19.
1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. Mem. Amer. Mus. Nat. Hist., vol. 9, pt. 6, pp. 289–567, figs. 1–18, pls. 42–52.
1910. On the skull of *Apternodus* and the skeleton of a new artiodactyl. Bull. Amer. Mus. Nat. Hist., vol. 28, pp. 33–42, figs. 1–5, pl. 6.
1913. A zalambdodont insectivore from the basal Eocene. *Ibid.*, vol. 32, pp. 307–314, figs. 1–6, pls. 60–61.
1937. Paleocene faunas of the San Juan Basin, New Mexico. Trans. Amer. Phil. Soc., new ser., vol. 30, pp. i–viii, 1–510, figs. 1–85, pls. 1–65.
MILLER, GERRIT S., JR.
1929. A second collection of mammals from caves near St. Michel, Haiti. Smithsonian Misc. Coll., vol. 81, no. 9, pp. 1–30, pls. 1–10.
MIVART, ST. GEORGE
1867–1868. Notes on the osteology of the Insectivora. Jour. Anat. Physiol., vol. 1 (1867), pp. 281–312, 11 figs.; vol. 2 (1868), pp. 117–154, 6 figs.
1871. On *Hemicentetes*, a new genus of Insectivora, with some additional remarks on the osteology of that order. Proc. Zool. Soc. London, pp. 58–79, figs. 1–9, pl. 5.
MOHR, ERNA
1936a. Biologische Beobachtungen an *Solenodon paradoxus* Brandt in Gefangenschaft. I. Zool. Anz., vol. 113, pp. 177–188, figs. 1–17.
1936b. Biologische Beobachtungen an *Solenodon paradoxus* Brandt in Gefangenschaft. II. *Ibid.*, vol. 116, pp. 65–76, figs. 18–35.
1951. Lebensdauer einiger Tiere in Zoologischen Garten. Zool. Garten, vol. 18, p. 60.
MURRAY, ANDREW
1866. The geographical distribution of mammals. London, Day and Son, Ltd., xvi+420 pp., 1 pl., 101 maps.
OSBORN, HENRY FAIRFIELD
1907. Evolution of mammalian molar teeth. Edited by W. K. Gregory. New York, the Macmillan Co., ix+250 pp., 215 figs.
PARKER, WILLIAM KITCHEN
1886. On the structure and development of the skull in the Mammalia. Parts II, Edentata, and III, Insectivora. Phil. Trans. Roy. Soc. London, vol. 176, pp. 1–275, pls. 1–39. (Edentata, pp. 1–119, pls. 1–15; Insectivora, pp. 121–275, pls. 16–39.)
PATTERSON, BRYAN, AND PAUL O. MCGREW
1937. A soricid and two erinaceids from the White River Oligocene. Publ. Field Mus. Nat. Hist., geol. ser., vol. 6, no. 18, pp. 245–272, figs. 60–74.
PETERS, WILHELM
1864. Ueber die Saugethier-gattung *Solenodon*. Abhandl. K. Akad. Wiss. Berlin, for 1863, pp. 1–22, pls. 1–3.
PETERSON, OLOF AUGUST
1917. Report on the fossil material collected

in 1913 by the Messrs. Link in a cave in the Isle of Pines. Ann. Carnegie Mus., vol. 11, pp. 359–361, pl. 36.

POEY, FELIPE
1851. Memorias sobre la historia natural de la Isla de Cuba. Havana, Barcina, vol. 1, 463 pp., 34 pls.

ROUX, G. H.
1947. The cranial development of certain Ethiopian "insectivores" and its bearing on the mutual affinities of the group. Acta Zool., vol. 28, pp. 165–397, figs. 1–69.

RUDD, ROBERT L.
1955. Age, sex, and weight comparisons in three species of shrews. Jour. Mammal., vol. 36, pp. 323–339, figs. 1–6, 1 table.

SABAN, ROGER
1954. Phylogenie des insectivores. Bull. Mus. Natl. Hist. Nat., Paris, vol. 26, pp. 419–432.

SCHAEFFER, J. PARSONS (ED.)
1942. Morris' Human anatomy. Tenth edition. Philadelphia, Blakiston Co., xi+1641 pp., 1155 figs.

SCHLAIKJER, ERICH MAREN
1933. Contributions to the stratigraphy and palaeontology of the Goshen Hole area, Wyoming. I. A detailed study of the structure and relationships of a new zalambdodont insectivore from the middle Oligocene. Bull. Mus. Comp. Zoöl., vol. 76, no. 1, pp. 1–27, figs. 1–8, 1 pl.
1934. A new fossil zalambdodont insectivore. Amer. Mus. Novitates, no. 698, pp. 1–8, figs. 1–3.

SCHLOSSER, MAX
1887. Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des Europäischen Tertiärs. Pt. I. Beitr. Paläont. Geol. Osterreich-Ungarns, vol. 6, pp. 1–224, pls. 1–5.

SCOTT, WILLIAM BERYMAN
1903–1905. Reports of the Princeton University expeditions to Patagonia 1896–1899. Volume V. Mammalia of the Santa Cruz beds. I. Edentata. II. Insectivora. III. Glires. Princeton, New Jersey, the University, xi+499 pp., 49 figs., 71 pls.

SCOTT, WILLIAM BERRYMAN, AND GLENN LOWELL JEPSEN
1936. The mammalian fauna of the White River Oligocene Part I. Insectivora and Carnivora. Trans. Amer. Phil. Soc., new ser., vol. 28, pt. 1, pp. 1–153, figs. 1–7, pls. 1–22.

SIMPSON, GEORGE GAYLORD
1927. A North American Oligocene edentate. Ann. Carnegie Mus., vol. 17, pp. 283–298, pl. 24.
1928. Affinities of the Mongolian Cretaceous insectivores. Amer. Mus. Novitates, no. 330, pp. 1–11, fig. 1.
1929. A new Paleocene uintathere and molar evolution in the Amblypoda. *Ibid.*, no. 387, pp. 1–9, figs. 1–9.
1931. A new classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 59, pp. 259–293.
1941. A new Oligocene insectivore. Amer. Mus. Novitates, no. 1150, pp. 1–3, fig. 1.
1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. i–xvi, 1–350.

SISSON, SEPTIMUS
1938. The anatomy of the domesticated animals. Revised by James Daniels Grossman. Third edition, revised. Philadelphia and London, W. B. Saunders Co., 972 pp., 737 figs.

STEHLIN, HANS G.
1940. Zur Stammesgeschichte der Soriciden. Eclog. Geol. Helvetiae, vol. 33, pp. 298–306, figs. 1–5.

STORY, H. ELIZABETH
1951. The carotid arteries in the Procyonidae. Fieldiana: Zool., vol. 32, pp. 477–557, figs. 82–98.

TRUE, FREDERICK W.
1897. A revision of the American moles. Proc. U. S. Natl. Mus., vol. 19, no. 1101, pp. 1–111, figs. 1–46, pls. 1–4.

VAN DER KLAAUW, C. J.
1931. The auditory bulla in some fossil mammals. Bull. Amer. Mus. Nat. Hist., vol. 62, pp. 1–352, figs. 1–18.

WEGNER, R. N.
1951. Unterschiede der Nasenlochgestaltung und des Os nariale bei den Säugetieren (*Choloepus*) und den Bauriamorphen. Anat. Anz., vol. 97, Ergänzungsheft, pp. 104–111, figs. 1–7.

WINGE, HERLUF
1941. The interrelationships of the mammalian genera. Translated from the Danish by E. Deichmann and G. M. Allen. Copenhagen, C. A. Reitzels Forlag, vol. 1, xii+418 pp., 2 figs., 1 pl.

WISLOCKI, G. G.
1940. The placentation of *Solenodon paradoxus*. Amer. Jour. Anat., vol. 66, pp. 497–531, fig. 1, pls. 1–7.

WITTE, GASTON-FRANCOIS DE, AND SERGE FRECHKOP
1955. Sur une espèce encore inconnue de mammifère africain, *Potamogale ruwenzorii*, sp. n. Bull. Inst. Roy. Sci. Nat. Belgique, vol. 31, no. 84, pp. 1–11, figs. 1–4.

WOODWARD, M. F.
1896. Contributions to the study of mammalian dentition.—Part II. On the teeth of certain Insectivora. Proc. Zool. Soc. London, pp. 557–594, figs. 1–2, pls. 23–26.